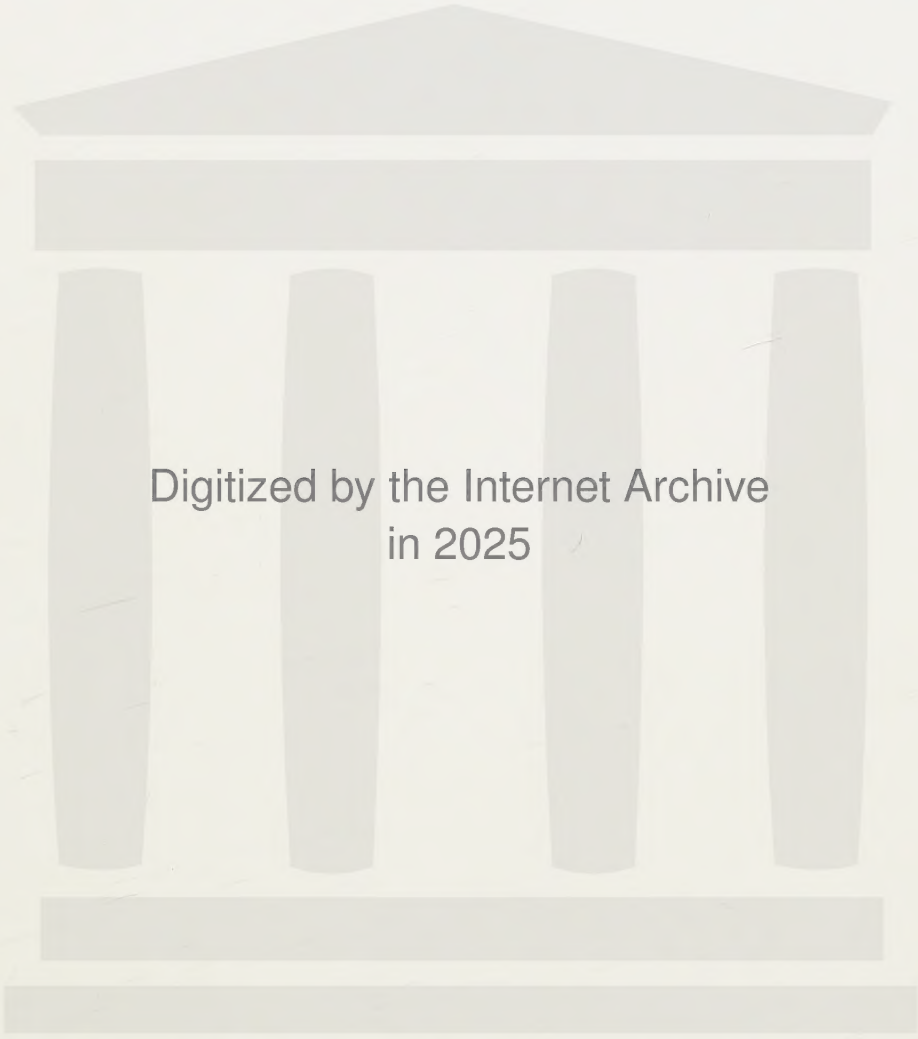
LOCUSTS AND GRASSHOPPERS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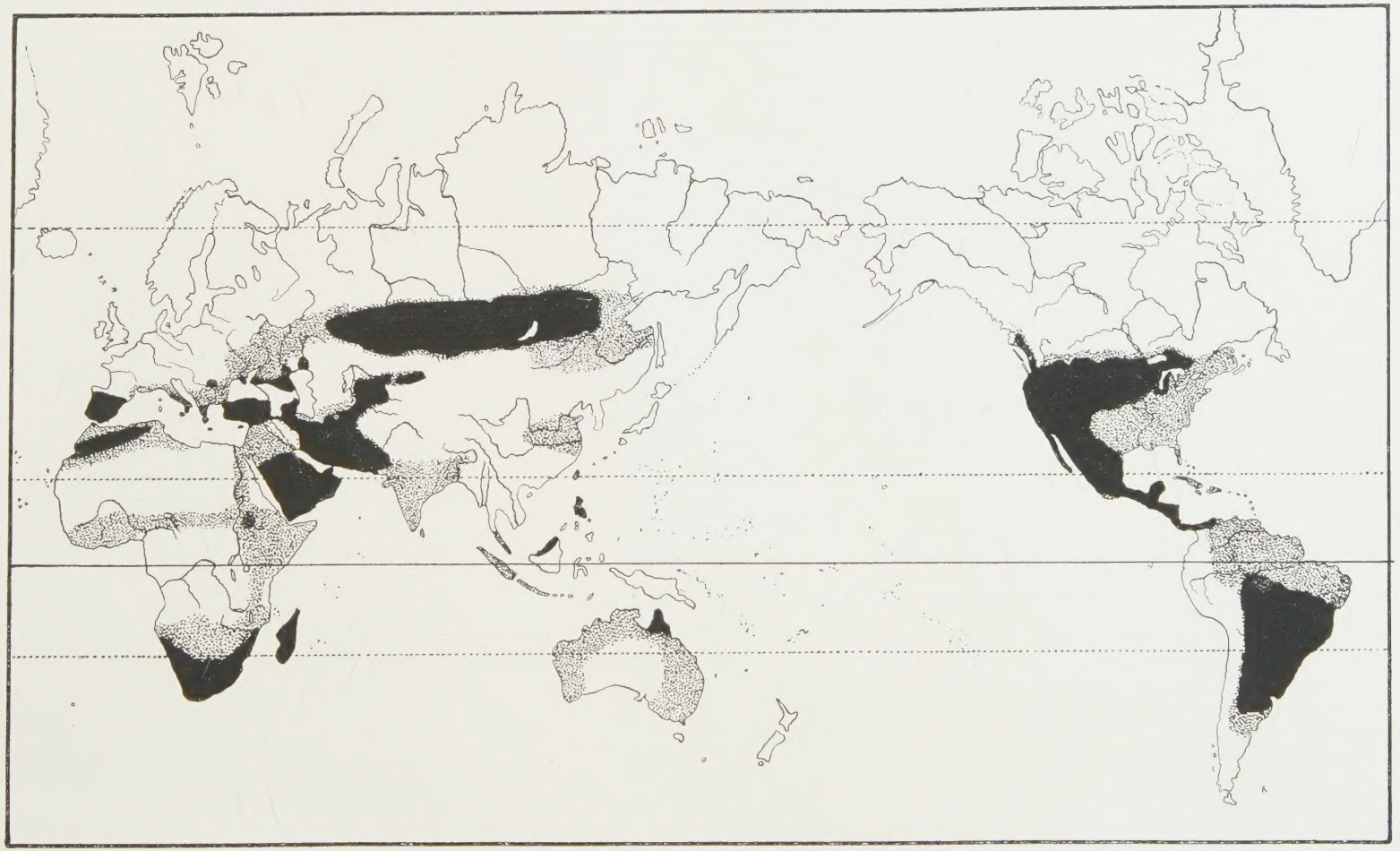

LOCUST AND GRASSHOPPER AREAS OF THE WORLD. [*Frontispiece*

The black areas are subject to regular plagues of locusts and grasshoppers; the dotted areas are invaded occasionally.

LOCUSTS AND GRASSHOPPERS

A HANDBOOK FOR THEIR STUDY AND CONTROL

BY

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PREFACE

It would be difficult to say when man first met with the "locust problem," but it certainly happened at the earliest dawn of agriculture, when he first attempted to disturb the soil and to compel it to produce the plants he required. Proof of the accuracy of this statement may be found in the presence of locusts and grasshoppers as pests in the countries that are even now still at that primitive stage of human culture, as for instance some areas in Central Africa. Moreover, even the most ancient monuments of human civilisation, such as those of Assyria and Egypt, offer some definite beginnings of locust "literature," reflecting contemporary ideas of the insects and stressing the economic rôle played by them even in those remote times. This rôle has increased steadily in importance with the progress of agriculture, which, while it has not yet materially reduced the areas suitable for these insects, provides them with enormous resources in the shape of suitable food. In all continents without exception and in many different countries, the inter-relations of man with these insects have assumed the character of a continuous struggle, that has fluctuated in intensity, for the very existence of agriculture, and it has not been one in which man has always been victorious. In the great majority of cases this struggle has merely assumed the character of desperate attempts to save from destruction at least a portion of the crops, and up till quite recently, there has been no chance for man to adopt a definitely aggressive policy against the insects. It is only with the general progress of agriculture and reduction of uncultivated areas to a minimum that the locust problem in some few countries, such as Western Europe or North America, has lost its permanency, and the outbreaks have become far less regular, though still exceedingly dangerous owing to the increased value of crops. Other countries are at present either at the most critical stage when the uncultivated areas provide suitable breeding grounds for locusts while the crops are of great value and in constant danger (South Africa, Russia, South America), or else they are only just beginning to feel the menace that locusts bring to the development of agriculture (Australia).

No figures sufficiently exact or reliable exist to show the extent of locust ravages and the cost of the control measures in all the countries concerned, but for instance, in South Africa alone, the cost of control has reached over £500,000 per annum in some recent years, not including the value of the unpaid labour supplied by the farmers. Devastations of all crops over large areas, with the resulting famine, are a commonplace in the annals of almost

every country subject to locust attacks. All this is so well known that it does not seem worth while dwelling on the point, the enormous economic importance of the insects in question being beyond any doubt.

It is only natural to ask what are locusts, how do they live and how can they best be controlled ? To obtain an answer to these simple questions is, however, not an easy matter, since, strange as it may seem, no comprehensive and up-to-date account of these insects exists. The literature dealing with locusts and grasshoppers is stupendous (larger than that on any other single group of insects), and is very widely scattered over hundreds of books, pamphlets, magazine articles, etc., published in a score of languages. To find answers to one's questions in this mass of literature is often impossible and always very difficult, and an attempt to collate all available information on the problem should not be out of place.

The present book represents nothing more than an attempt of this kind, and its aim is to present a general survey of the accumulated knowledge on locusts and grasshoppers, their bionomics and the theory and practice of their control. It would not be a practical policy to restrict the book to a mere survey of the technique and organisation of control, since the first encounters with the locust and grasshopper problem in practice will show any one that the only way to its solution lies in a thorough knowledge of the insects themselves and in an understanding of their interrelations with their environment. This knowledge is mainly notorious for the numerous lacunæ in it. To fill these a large amount of research work is urgently needed, and this book aims at pointing out not only what is known, but what should be investigated in the first instance, in order to approach at least a few steps nearer to a practical solution of the locust problem. The latter is remarkable for having very many sides to it, and this I hope to demonstrate, but special stress is laid throughout the book on one particular aspect of the problem—that of the great importance in the life of the insects and in their economic relations to man of the actual conditions of their environment in the broadest sense of the word. I have tried to apply as widely as possible this ecological method in the study of locusts and grasshoppers, but without much success, owing to the appallingly low standard of our knowledge in this direction. In any case I hope that I shall at least succeed in demonstrating the rôle and importance of the ecological method so that it can be put to the test by those immediately concerned in the locust problem.

On the practical side of locust and grasshopper control, I have tried to emphasise the importance of suitable organisation, which is very often neglected, too much reliance being placed on the purely technical side of control measures ; these, however, cannot be successful if the organisation of their application is not satisfactory.

The book may be thus characterised as an attempt to produce a handbook on locusts and grasshoppers that will be of some use in the study of these insects and in their control to entomologists and all concerned in the problem. The magnitude and difficulties of this task are obvious, and only the fact that it has been possible for me to become acquainted with practically the whole

literature on the question has decided me to make the attempt. The book, however, does not represent a mere compilation of the literature; all the information gained from it has been subjected to a critical analysis and a great deal of it rejected altogether, while my personal experience with locusts and their control has been sufficiently wide to justify my action. This experience emboldens me to advance some new points of view on various facts and some new theories; if some of these should prove to be insufficiently founded, they will at any rate serve as working hypotheses and as stimuli for further investigations.

One point requires special mention. This is the exact definition of the terms "locust" and "grasshopper" which I have attempted to maintain throughout the book. While both are members of the family ACRIDIDÆ, or short-horned grasshoppers in the broad sense, I propose to restrict the name "locust" only to such species as definitely possess gregarious habits and wander or migrate in swarms; under "grasshoppers" in the more narrow sense of the word, I understand non-gregarious and non-migrating species. This definition of the word "locust" should not meet with any objections, while it is high time to put an end to a loose use of it which is devoid of any special meaning.

The original edition of the book was published in Russian in 1927 at Moscow, by the Central Cotton Committee, but the present English edition differs essentially from it. The general part remains practically the same with some additional data, particularly in the article on spermatophore fertilisation. The chapter on natural enemies has been expanded to include parasites and other enemies known from all countries (only Palæarctic species being recorded in the Russian edition), while some fresh information has been incorporated in the articles on Hymenopterous egg-parasites, larviparous flies, Gordiacea, and Gregarines. The chapter on the technique of control has been supplemented by some information on mechanical methods little used in Russia, but favoured in other countries. The chapter on the organisation of control has been completely rewritten to suit the varying conditions of different countries. Finally, the whole of the special part (Chapters X to XIX) is specially written for the English edition, since in the Russian one it was represented by only four chapters instead of ten, though, on the other hand, the Russian species were treated there more fully. The bibliography at the end has also been materially increased.

The work could not have been accomplished were it not for the kind assistance received from many sides. First of all I have great pleasure in acknowledging my deep gratitude to my numerous colleagues in various countries, who have not only supplied me with copies and reprints of their papers, often published in not readily accessible local periodicals, but often also offered to put at my disposal information not yet published. The chapter on the natural enemies of ACRIDIDÆ has been compiled with the friendly assistance of some colleagues in the British Museum; in this connection I am particularly grateful to Dr. H. A. Baylis and Mr. S. Hirst. My study of the literature has been almost entirely accomplished in the excellent library

of the Imperial Bureau of Entomology and made easy by the ready assistance given me by the librarian, Mr. C. J. Golledge, whose wide knowledge of entomological literature has saved me much time and trouble. A number of colleagues have supplied me with illustrations, and I am particularly grateful for this to my friends, Mr. V. V. Nikolsky, Mr. V. I. Plotnikov, Mr. Alexei N. Kiritchenko, Mr. H. B. Johnston, and Mr. P. A. Sviridenko. I am obliged to the Wellcome Tropical Research Laboratories for the loan of originals of Plates VIII and IX, and to the publishing firm of Paul Parey, Berlin, for permission to reproduce the figures on Plate VI taken from Bücher's book on locusts in Anatolia. The sources from which the other illustrations are taken are acknowledged under the respective figures.

My greatest debt of gratitude is that to Dr. S. A. Neave, who has undertaken the laborious and thankless task of reading through the manuscript, correcting its style (which was badly needed) and seeing the book through the press ; many improvements are due to his useful suggestions. I also wish to thank Miss R. Davenport for her assistance in reading the proofs and in the preparation of the index.

B. P. UVAROV.

London, October 1928.

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GENERAL PART

CHAPTER I

EXTERNAL MORPHOLOGY

The body of the Acrididæ, as that of other insects, may be divided into three main sections—head, thorax, and abdomen (Fig. 1), each of them bearing certain appendages.

Head.—The head has a more or less oval shape, and only in some species does it become conical (Pyrgomorphinæ, *Acrida*). The anterior surface of the head is called the *front*, and it may be either vertical or oblique in profile,

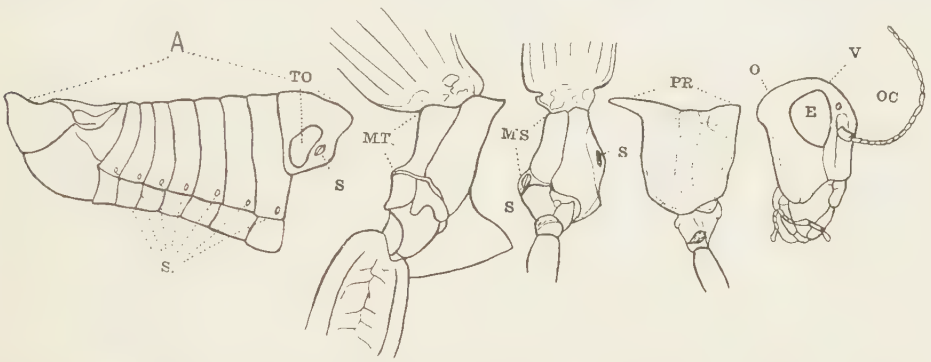

Fig. 1.—Diagrammatic representation of the body of an Acridid.—V, vertex.—O, occiput.—Oc, ocellum.—E, compound eye.—Pr, pronotum.—S, spiracles.—Ms, mesothorax.—Mt, metathorax.—A, abdomen.—TO, tympanal organ (after Packard).

and in the latter case it forms an acute angle with the upper surface of the head. Along the front runs a raised *frontal ridge*, which may be either flat or furrowed. The upper surface of the head between the large eyes and in front of them is called the *vertex* (Fig. 1, V), and it may be either horizontal or more or less sloping forward. The margins of the vertex are often well raised and sharp, but they are sometimes fairly broad; in the latter case they often bear regular depressions, which are called the *foveolae* of the vertex and are greatly used in systematics. The part of the head behind the compound eyes is called the *occiput* (Fig. 1, O).

Apart from the always very large *compound eyes* (Fig. 1, E), there are also *simple eyes* or *ocelli*, usually three in number—one placed at the middle of the frontal ridge, a little lower than the base of antennæ, and two paired lateral ocelli, which are close to the upper front margin of the compound eyes (Fig. 1, Oc).

The appendages of the head are the antennæ and the mouth-parts.

The *antennae* of all locusts and grasshoppers consist of a relatively small number (not more than 28) of fairly large and distinctly separated joints. The length of the antennæ very seldom exceeds that of the whole body, but usually they are considerably shorter, and this is a character by which ACRIDIDÆ may always be easily separated from the, so-called, long-horned grasshoppers (TETTIGONIIDÆ), in which the antennæ consist of a very large number of scarcely distinguishable small joints and are usually much longer than the body. As regards their shape, the antennæ of locusts and grasshoppers are usually filiform, *i.e.* fine, round, and equally broad throughout, but in some species the antennæ are ensiform (flattened and dilated near the base, *Acrida*), or clavate (with a club at the end, *Gomphocerus*). As the antennæ are presumably the seat of some sense organs (see p. 25), these modifications of structure must be of some biological significance.

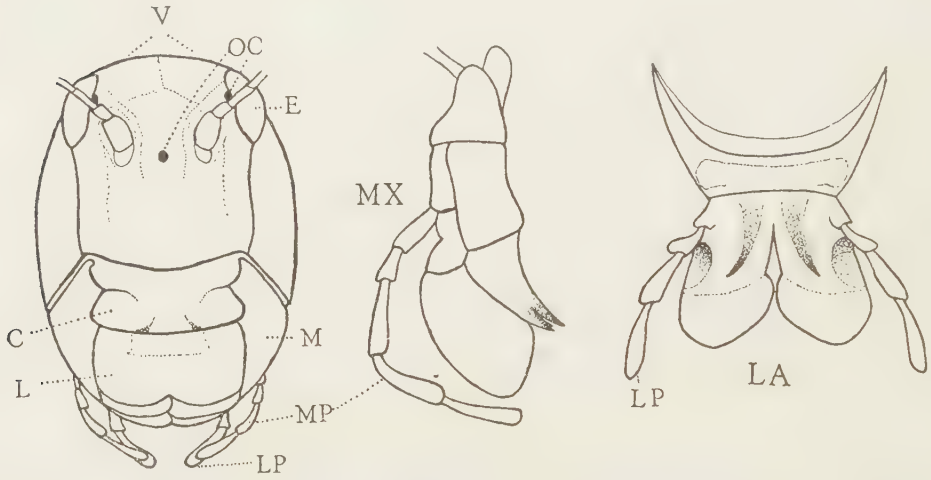

FIG. 2.—Head, seen from the front, and the mouth parts of *Locusta migratoria*.—V, vertex.—Oc, ocelli.—E, compound eye.—C, clypeus.—L, labrum.—M, mandible.—Mx, maxilla.—MP, maxillary palpi.—LP, labial palpi.—La, labium (after Chang, with alterations).

The *mouth-parts* (Fig. 2) are typical of biting insects and consist of a pair of mandibles (M), a pair of maxillæ (Mx), with maxillary palpi (MP), labium (La) with labial palpi (LP) and labrum (L). The mandibles are very strongly developed, strongly chitinised, and, in connection with their powerful muscles, represent a formidable cutting and biting apparatus. The mandibles are not bilaterally symmetrical, the right one differing from the left in shape (Fig. 3). Particularly interesting are the extremities of the mandibles, by which they touch each other; these surfaces are most strongly chitinised and provided with a series of teeth, the shape of which is very typical for different species (Petrov, 1905, has given detailed descriptions and figures of the mandibles and of the mouth-parts generally of many Russian species).

The **Thorax,** as it is seen after the wings and elytra are removed, consists of three segments—prothorax, mesothorax, and metathorax (Fig. 1, Pr, Ms, Mt), each of them bearing a pair of legs. The first of these segments can be,

in fact, seen without removing the elytra and wings, because its dorsal part is strongly developed and forms the *pronotum*—a roof-shaped plate, covering the whole prothorax from above. The whole of the pronotum is formed as the result of an extensive development of the upper portion of the prothorax, as it may be seen after boiling the insect in caustic potash, when the pronotum may be separated from the thorax proper of which it only forms a covering (Crampton, 1918). The shape and details of the structure of the pronotum are of great importance in the systematics of ACRIDIDÆ, special attention being paid to its raised ridges (median and lateral keels) and to the transverse furrows. These furrows are often considered to be traces of segmentation of the prothorax, but Crampton (1918) has shown that they do not correspond

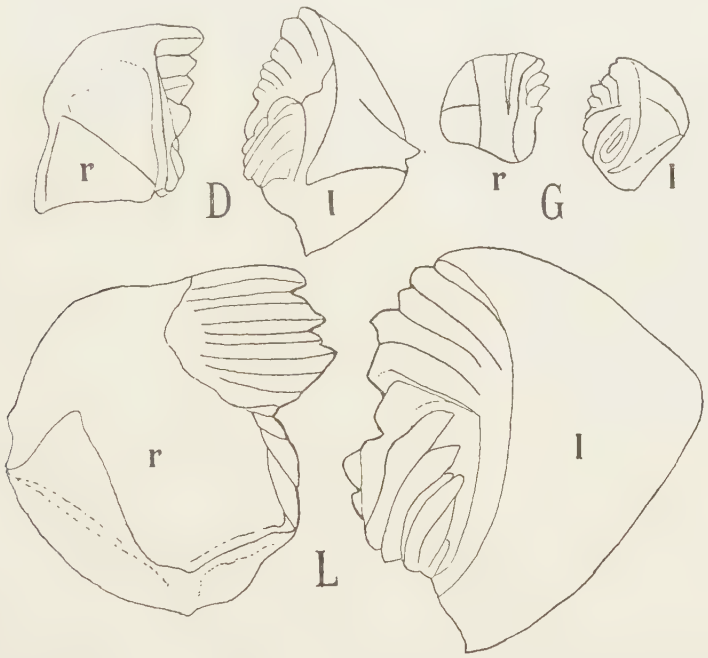

FIG. 3.—Right (*r*) and left (*l*) mandibles of *Dociostaurus maroccanus* (D), *Gomphocerus sibiricus* (G), and *Locusta migratoria* (L) (after Petrov).

to the intersegmental furrows which can be seen on the prothorax after it has been macerated in caustic potash and the pronotum removed.

The lower surface of the prothorax or the prosternum (which is between the bases of the front legs) is more deeply sunk than that of the mesosternum and metasternum. In some groups of ACRIDIDÆ the prosternum is provided with a raised tubercle or spine of different shape ; it has apparently no biological significance, but nothing can be said definitely on this point, since the anatomy of this structure has never been studied.

The two following segments of the thorax, the mesothorax and metathorax, bear, in addition to the legs, the elytra and wings, respectively. The upper surface of these two segments is feebly chitinised, and their further segmentation remains visible (Fig. 1). In the soft, feebly chitinised membrane

between the segments lie spiracles (S). (For a detailed description of the structure of the thorax, see Crampton, 1918.)

The *legs* of the ACRIDIDÆ are very simple in structure. The front and the middle pair are of similar structure, and each consists of the following parts, beginning from the base : *coxa*, *trochanter*, *femur*, *tibia*, and *tarsus* (Fig. 4). The coxæ (C) and especially the trochanters (Tr) are very small ; the front coxæ are often armed with a curved spine. The tibiæ are usually armed with several small spinules below and at the apex, and they are more or less cylindrical in shape ; an exception is presented by the male of the Siberian grasshopper (*Gomphocerus sibiricus*, Fig. 95), which has the front tibiæ inflated like a pear ; neither the possible biological significance of this structure nor even its anatomy are known. The tarsus (Ta) consists of three joints ; the terminal joint bears a pair of *claws* (Cl), between which there is a *pulvillus* (P). The latter helps the insect in climbing, and it is, accordingly, more strongly developed in those species that always live on plants (phytophils), while it is scarcely perceptible in the species living on the ground (geophils).

The hind legs (H) consist of the same parts as the two other pairs, but differ in their considerably larger size. The trochanters are very small and practically fused with the coxæ, and are visible only when looked at from below. The femora, on the contrary, are very large and stout ; within them are placed the strong muscles used for jumping. In some groups of ACRIDIDÆ the jumping legs are relatively feebly developed, but they are always longer than the other two pairs. On the inner face of the hind femora there are special structures for producing sound, and these will be dealt with later.

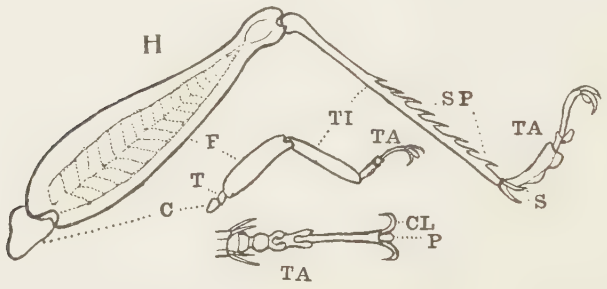

FIG. 4.—Legs of an Acridid.—H, hind leg.—C, coxa.—T, trochanter.—F, femur.—Ti, tibia.—Ta, tarsus.—Sp, spines.—S, spurs.—Cl, claws.—P, pulvillus (after Chang).

The hind tibiæ also differ considerably in size from the front and middle ones, while they are quite or nearly as long as the hind femora. They are usually round in section, but in some species living near water and swimming occasionally (*Oxya*, certain TETRIGIDÆ), they are flattened and expanded near the apex. Each tibia is armed along the margins of its upper side with two rows of rigid acute *spines* (Sp) ; at the apex itself, there are two pairs of *spurs* (S), which are joined to the tibia in such a manner as to be movable ; these are used when making a jump, and they are particularly strongly developed in species living on loose sand (*Hyalorrhipis*, *Leptopternis*).

Of the two pairs of *wings*, the front ones are fixed to the mesonotum and are called the *elytra*. They are relatively hard, leathery, not folding, and scarcely or not at all transparent. The hind wings are more delicate, transparent (sometimes brightly coloured), and folding like a fan under the elytra.

Both on the wings and on the elytra there is a complicated system of longitudinal and transverse veins which are given special names. A study of the venation is of great importance in the systematics of these insects, but for our purposes it may be left out of consideration.

The elytra are usually better developed and provided with a more regular system of veins in the males; in the females they are, as a rule, shorter and with a simpler venation. This fact is connected with the capacity for stridulation, which is usually confined to the male sex, and the expanded elytra serve as a sounding board (see below, p. 29).

In many species an incomplete development of the elytra and wings may be observed. The first stage of the incomplete development of wings is when the male has the organs of flight perfectly developed, while those of the female are shortened and useless for flying (certain species of *Arcyptera*, *Psophus stridulus*). The difference between the two sexes in this case may be enormous, as, for example, in the South African grasshoppers of the subfamily PAMPHAGINÆ, in which the male has very large elytra and wings, while the female has lost absolutely all traces of either. In other cases neither sex is able to fly, though the male may have well-developed elytra, but quite rudimentary wings (*Chorthippus parallelus*, *C. curtipennis*). The reduction of the organs of flight has gone still further in other species, in which the wings are absent, or practically so, while the elytra are represented by scale-like structures on the sides of the mesonotum (females of the two species of *Chorthippus* mentioned above, *Podisma*, certain species of *Melanoplus*, etc.). Finally, there are many species in which no trace of elytra or wings can be seen (many of the PAMPHAGINÆ a.o.).

The reduction of the organs of flight has some connection with the conditions of environment that is not yet clear. Thus the species living on high mountains are nearly all wingless, or at least flightless owing to insufficiently developed wings. On the contrary, in the fauna of desert plains there are hardly any species with abbreviated elytra, and the majority of the desert ACRIDIDÆ are very good fliers. Morse (1904) pointed out that in the North American fauna there is a definite predominance of flightless forms among the ACRIDIDÆ living in forest or shrub habitats, while the grasslands are populated mainly by good fliers. He is inclined to account for this by the inconvenience to movement caused by the presence of long wings in dense vegetation, where crawling is the most convenient mode of progression; in open grasslands, ability to fly is on the contrary very useful to the insects. These considerations are, however, too theoretical to help the elucidation of the problem.

In some short-winged ACRIDIDÆ forms with the organs of flight fully developed may be occasionally observed; this happens, for instance, fairly often in the European flightless grasshopper (*Podisma pedestris*), the macropterous form of which is not very uncommon. As pointed out by Karny (1912), such a return to the macropterous condition is only possible for a species in which the process of reduction of the organs of flight has not gone too far; it does not happen with an entirely apterous species or with one in which the wings

and elytra are quite rudimentary. The venation of the elytra in such macropterous forms is usually somewhat irregular and simplified. The factors causing the appearance of macropterous forms are not clear, but they must have some connection with the conditions of the development of the larvæ. Thus, Hancock (1894) records cases of the mass appearance of the macropterous forms of *Tettigidea lateralis* after abnormally hot and dry weather. More exact data can be obtained only by means of special laboratory experiments.

The **abdomen** of the ACRIDIDÆ consists of several segments, connected by feebly chitinised elastic membranes (Fig. 1, A). Each segment is clearly divided into an upper and a lower half, called tergite and sternite, respectively. At the lower margin of each tergite a small opening, a *spiracle* (S), may be seen, while the first tergite bears a large structure—the tympanal organ (TO, see

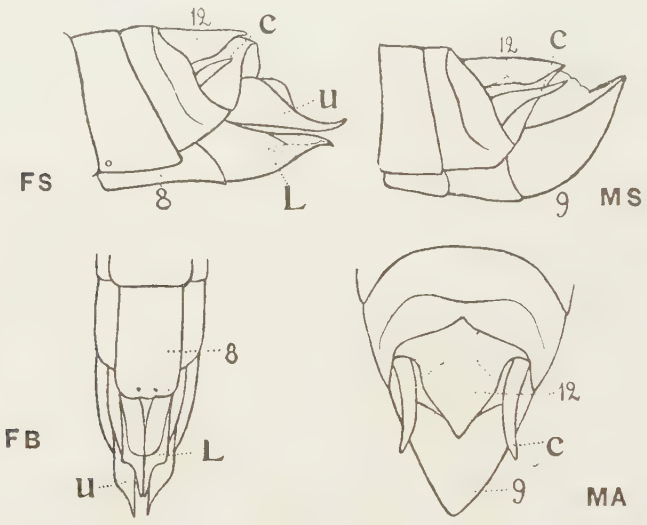

FIG. 5.—Extremity of abdomen in the two sexes of *Locusta migratoria*.—FS, abdomen of female, side view.—FB, do. from below.—MS, do. of the male, side view.—MA, do. from above.—C, cercus.—U, upper valve of the ovipositor.—L, lower valve of the ovipositor.—8, subgenital plate of female.—9, do. of the male.—12, supra-anal plate. (After Chang, with alterations.)

p. 27). The number of visible segments is different in the two sexes, while, even in the same sex, their arrangement is different on the dorsal and ventral side. In the male (Fig. 5, MS, MA) there are 10 tergites, but the two last may be partly or wholly fused; the next, 11th tergite, is not visible from above, and it serves for the formation of certain internal parts; the 12th tergite is represented by the so-called *anal plate*. Laterally to the anal plate are placed the paired one-jointed *cerci* (C). On the ventral surface, nine sternites are visible, the first being fused with the metasternum, but still distinguishable from it; the 9th sternite forms the so-called *genital plate*, an inflated structure in the cavity of which the copulatory apparatus is concealed. The abdomen of a male, thus, always terminates in a more or less conical, or obtuse, genital plate.

In the female (Fig. 5, FS, FB), the tergites are also ten in number, and the

12th forms an *anal plate*, while on the ventral side there are only eight sternites, the 8th being usually considerably longer than the others and called the *genital plate*. The tip of the female abdomen is formed by the two pairs of *valves* of the *ovipositor* (U, L), which resemble strong chitinous hooks or appendages; it is therefore very easy to distinguish the sexes. The shape of the ovipositor varies in different species in accordance with the conditions under which the eggs are laid, since its function is to prepare the hole for the eggs. In the species that insert their eggs into the ground the ovipositor has its valves shaped like strong hooks, while in those species that lay their eggs in the stems of plants, the valves are built on the principle of a saw.

Integuments.—The whole body of the ACRIDIDÆ, as in all other insects, is covered by a strong layer of chitin, which forms the external skeleton, the muscles being attached to its internal processes or endo-skeleton. The chitinous covering of these insects is not so strong as, for instance, that found in beetles, while in the intersegmental membranes it is quite soft and elastic. On the surface various sculptures may be observed, such as impressed dots, wrinkles, or furrows; as a rule, the sculpture is more pronounced in the species that live on the ground, especially in open desert countries. In such desert grasshoppers the integument is often covered by strong wrinkles, ridges, tubercles and spines; the integuments in these cases are usually coloured like the ground, and this makes the insect exceedingly difficult to see there. On the contrary, in grasshoppers that live in the grass, the integuments are usually without a pronounced sculpture, and green and yellowish-green tones predominate.

The colour of the integument depends on pigments of various kinds, deposited partly in the chitinous layer, partly under it. The physiological importance of pigments must be very great; later we shall see that on the coloration depends the body temperature, which itself largely determines all the most important manifestations of external activity. We shall also see that the deposition of certain kinds of pigments is directly connected with the activities of the insect and with the conditions of the environment. Respecting this great physiological importance of the pigments, we can, however, only speculate more or less successfully, since we possess no real knowledge of them, and do not even know their chemical nature. It may be conveniently pointed out here that the ACRIDIDÆ, with their exceedingly modifiable coloration, would provide an excellent object for biochemical studies on pigments, while the results of such studies would be of great advantage to the students of the bionomics of grasshoppers and locusts.

There are often some *hairs* on the surface of the bodies of grasshoppers, but they are seldom strongly developed; only in some desert species may a dense hairy covering be observed, but this is exceptional.

CHAPTER II

ANATOMY AND PHYSIOLOGY

While it would be really better to describe first the anatomical structures of these insects and then to present a comprehensive account of their physiology, I find myself unable to adopt this course for the very simple reason that our knowledge of the physiology of the Acrididæ is unexpectedly small, and the fragmentary information we possess can be more conveniently discussed side by side with the anatomical description of the various organs.

Digestive System

The alimentary tract of the Acrididæ is of a fairly uniform type throughout the group, and the following description is based mainly on a detailed study of the digestive system of the North-American *Dissosteira carolina* by Tietz (1923), with some remarks on the variations in structure known in other species.

When studying and describing the alimentary tract, it is impossible to indicate definitely the position of its different sections with regard to the external divisions of the body, since that position is liable to considerable changes, dependent on the filling of the tract with food and the elasticity of the walls of certain portions of the tract.

The most anterior region of the alimentary tract (Fig. 6, Bu) is formed by the *buccal cavity*. The hind wall of the cavity is, in part, represented by the *tongue*, or *hypopharynx*, which is a strongly chitinised organ, bearing fine spines with supposed gustatory functions. On the undersurface of the tongue, near its tip, may be seen the opening of the common salivary duct. This duct runs for a short distance backwards, then divides into two branches; these pass into the thorax and here give off a number of small branches to the white grape-like clusters of the *salivary glands* (Sa). These glands are relatively small and in structure are compound alveolar glands, without reservoirs.

The next section of the alimentary tract is the *oesophagus* (O), a short, slender tube, strongly curved, with its inner surface bearing longitudinal folds. The œsophagus becomes merged into the *crop* (Cr), but there is no sharp outwardly visible division between these two parts, especially in starved individuals, and the crop stands out distinctly as a sudden dilatation of the alimentary canal only if the insect has been well fed before dissection. Internally, however, both sections are most clearly defined, because the inner wall of the crop is provided with transverse ridges (SC). Along the tops of these ridges are distributed rows of spines that probably serve to retard the passage of the food into the next section and also to cut it into shreds.

The crop gradually widens backwards and passes, without an external demarcation, into the *gizzard* (G). Internally there is again a considerable difference in this organ, the inner walls of which are provided with a series of discontinuous folds, grouped in longitudinal rows and each bearing one or two teeth (SG).

Farther back, the gizzard is gradually narrowed, and at the hind end its

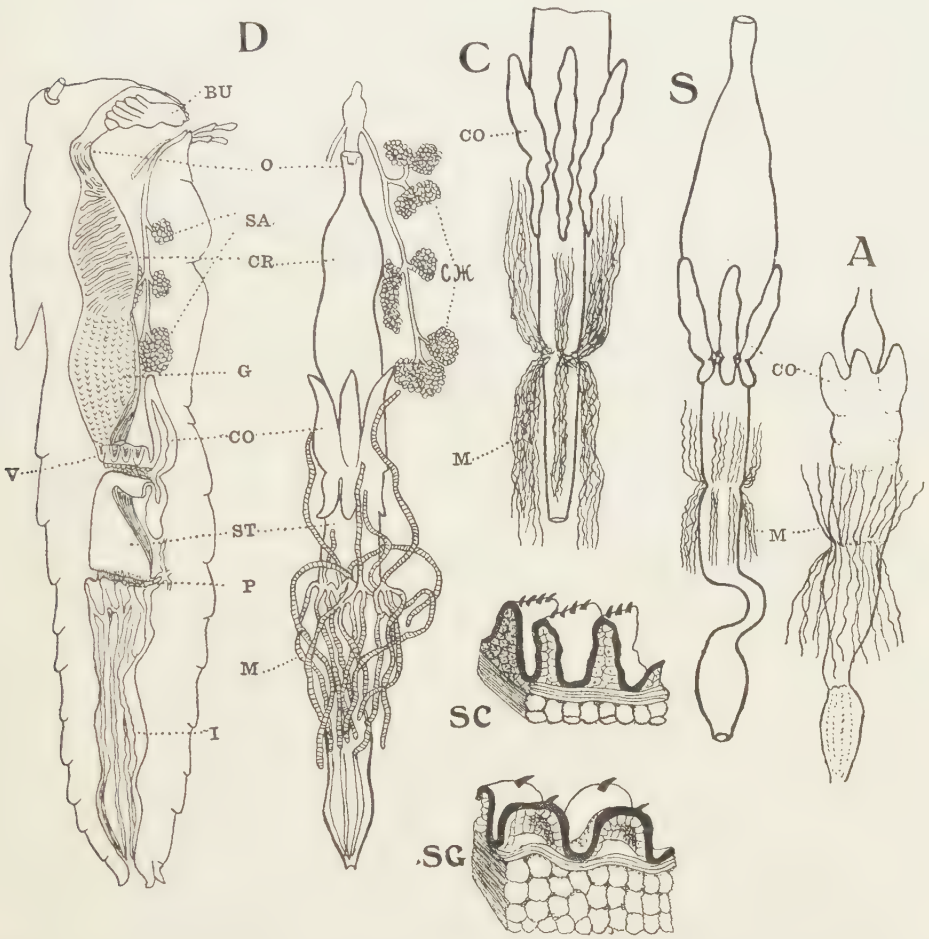

Fig. 6.—Alimentary canal of Acrididæ.—D, *Dissosteira carolina:* Bu, buccal cavity; O, œsophagus; Sa, salivary glands; Cr, crop; G, gizzard; Co, cœca; V, cardiac valve; St, stomach; P, pyloric valve; M, Malpighian tubes; I, intestine; SC, section of crop; SG, section of gizzard (after Tietz).—C, *Calliptamus italicus* (after Dufour).—S, *Stenobothrus* (after Dufour).—A, Tetrigid (after Robertson).

inner surface bears six V-shaped elevations, which together form the *cardiac valve* (V). This may prevent the food from passing too rapidly from the gizzard to the stomach, as well as preventing regurgitation of the food already in the stomach.

Next comes the *stomach* (St), or ventriculus. It may be recognised from the outside by its very thin, translucent walls and by the presence of the *gastric cœca* (Co). The latter are always six in number, and each is divided

into a long anterior and a short posterior portion; they take the form of blind pockets opening into the stomach. The walls of the stomach on the inner side are smooth and without a chitinous lining. Absorption of the food takes place both here and in the cœca, the soluble parts being absorbed in the cœca and fats by the cells of the epithelium of the stomach.

While the attachment of the gastric cœca marks outwardly the anterior boundary of the stomach, its posterior limit may be recognised by the attachment of the *Malpighian tubules* (M), which in function form a part not of the alimentary system, but of the excretory one. Internally, the boundary between the stomach and the intestine is formed by the *pyloric valve* (P), consisting of a transverse fold and of six round elevations; these, when the muscles of the intestinal wall contract, close the anterior end of the intestine, preventing the contents of the latter from re-entering the stomach.

The *intestine* (I) may be divided into three portions, not markedly separated outwardly, but differing in the structure of their inner walls, and, consequently, in their functions. The first section is the *ilium*, and it is a rather short, straight, tapering tube; its posterior diameter is about one-half that of the anterior end. The inner wall of the ilium is thrown up into numerous longitudinal folds, connected by oblique folds. These obviously serve to increase the absorptive surface.

The next section of the intestine, called the *colon*, is hardly recognisable from the ilium outwardly, but its inner structure differs by the presence of six longitudinal folds, not connected by oblique ones; the chitinous lining of the colon is thicker than that of the ilium.

A slight constriction marks the hind end of the colon and the beginning of the last section of the alimentary canal, the *rectum*. The latter is oval, tapering behind towards the anal opening. On its outer wall may be seen six longitudinal muscle bands, appearing as dark streaks; sometimes these bands extend to the colon walls as well. The inner wall of the rectum presents a continuation of the same six longitudinal folds as in the colon, but they are broader, less raised, and their intervals are much narrower; the surface of the rectal folds is smooth, and the chitinous layer thin. The rectum opens to the exterior through the anus which is placed above the genital opening.

Externally to the rectum, and firmly adherent to it, are six almost fused *rectal glands*, which are characterised by a strongly developed epithelial layer, consisting of large rectangular cells with large nuclei; their function is unknown.

Such is the structure of the alimentary tract in one typical grasshopper. In other species some modifications are observed, but typical of all Acrididæ are the relatively (when compared with the other Orthoptra) feeble development of the salivary glands, the absence of a separate muscular stomach, relatively straight alimentary canal, and the presence of six gastric cœca (in the Tettigoniidæ and in Gryllidæ there are only two).

Variation in the shape of the alimentary canal in the Acrididæ is most pronounced in that of the gastric cœca; thus, in *Stenobothrus* the posterior sections of the cœca are very short, almost rudimentary (Fig. 6, S), while in

Calliptamus italicus they are nearly as long as the anterior ones (Fig. 6, C). The colon and rectum are sometimes not straight, as described above, but sinuate (for example, in *Stenobothrus*, Fig. 6, S). The TETRIGIDÆ differ from other grasshoppers in that the gastric cœca are entirely without posterior sections (Fig. 6, A ; Robertson, 1916).

When the alimentary tract of the ACRIDIDÆ is compared with that of other Orthoptera, its relative shortness is very striking ; in most phytophagous animals the alimentary tract is known to be much longer than the body, while in the ACRIDIDÆ, which feed exclusively on vegetable food, this is seldom the case. Werner (1894) pointed out that only in one species did he find the length of the alimentary tract to exceed that of the body by one-seventh, while in the TETTIGONIIDÆ (mainly carnivorous) it is sometimes twice as long as the body. Apparently there is in this case no relation between the food and the length of the alimentary tract.

Physiology of Digestion.—The digestion of the ACRIDIDÆ has not been studied, but recently Bodine (1925*a*) has given some preliminary data on the hydrogen ion concentration in the various parts of the alimentary tract of grasshoppers. Certain aspects of the problem will be discussed later, in connection with the feeding habits (see p. 173).

RESPIRATORY SYSTEM

The respiratory organs of the ACRIDIDÆ include paired spiracles, a complex system of branched tracheæ and air-sacs.

The *spiracles* represent the outer openings of the respiratory system, through which the air enters it. The total number of spiracles is ten pairs, two being placed on the sides of the thorax and eight on the abdomen (Fig. 1, S). The first (mesothoracic) spiracle can be seen on the membrane connecting the prothorax with the mesothorax, and in the normal position it is covered by the projecting lateral margin of the pronotum. It is larger than the other spiracles, and two separate main tracheal tubes arise from it ; externally it is closed by a large two-lobed valve. The second (metathoracic) spiracle lies just above the coxal cavity of the middle leg, between the meso- and metathorax ; it is also provided with an external two-lobed valve. The third, or first abdominal, spiracle is situated in the cavity of the tympanal organ, close to the front margin of the latter. The remaining seven pairs of abdominal spiracles are all similarly placed on the lower front margin of each tergite up to the ninth, on which there is no spiracle ; they are all of the same structure and, unlike the thoracic spiracles, are provided with an internal occluding apparatus, while their outer orifice remains permanently open. The last of the abdominal spiracles is larger than the others.

The *tracheae*, as stated above, form a very complicated system within the body, and I will give here only a brief outline of the general scheme of their distribution (for a detailed description, see Vinal, 1919).

As regards structure, the tracheæ are elastic tubes of varying diameter, the walls of which consist of two layers, an epithelial layer and an inner chitinous layer. The latter (which is called the intima) is thickened at regular intervals

to form spiral threads, which serve to keep the tracheæ permanently open. These threads are absent in the finer branches of the tracheæ and in the air-sacs.

The tracheæ of the cephalic portion (Fig. 7, T) present a very complicated system of branches of the tube arising from the first spiracle. The main branches are as follows: the superior cephalic tracheæ (B), which forms branches in the upper parts of the head and a ring around the compound eyes;

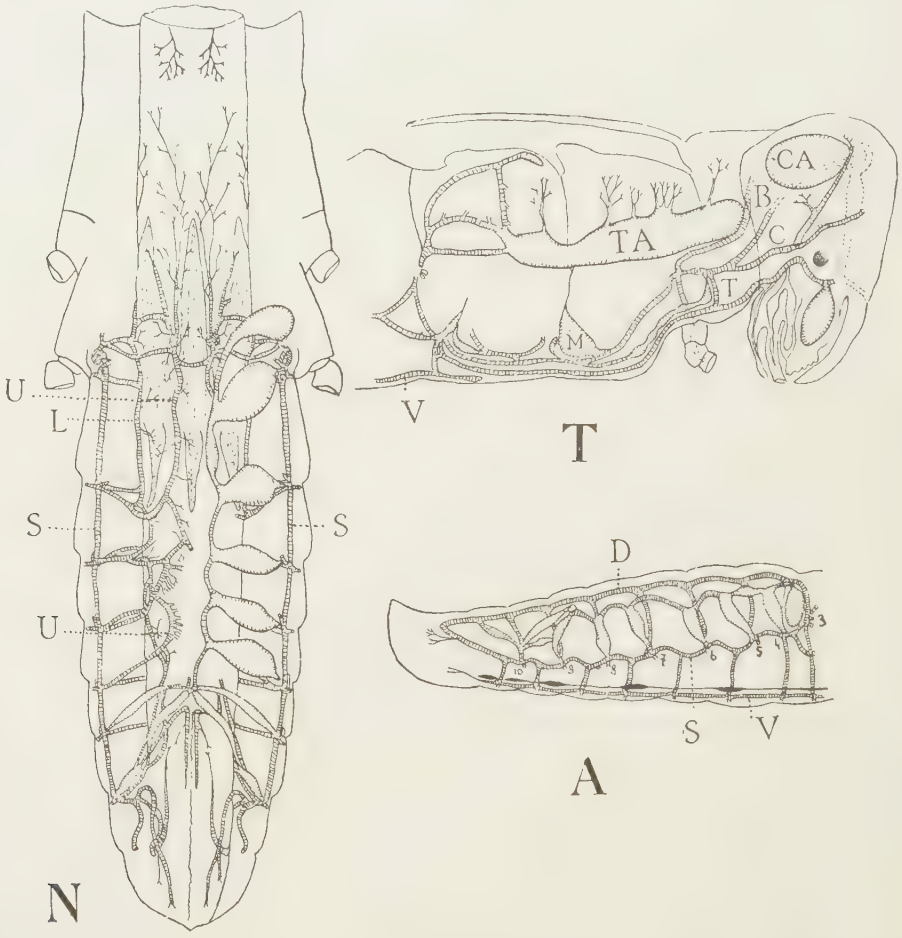

Fig. 7.—Respiratory system of *Dissosteira carolina*.—Horizontal longitudinal section of the body; tracheæ shown on one side, air-sacs on the other.—T, vertical longitudinal section of the head and thorax.—A, vertical longitudinal section of abdomen.—Tracheæ: S, spiracular; U, upper alimentary; L, lower alimentary; V, ventral; D, dorsal; B, upper cephalic; C, median cephalic; T, cephalothoracic.—Air-sacs: CA, cephalic; TA, thoracic; M, metathoracic (after Vinal).

the median cephalic tracheæ (C), with two branches, one of which brings air to the muscles of the sides of the head, while the other is directed upwards to the cephalic nerve ganglion, forms here a large number of vesicular air-sacs completely surrounding the ganglion and also emits branches to the anterior section of the alimentary tract and to a large cephalic air-sac (CA); the cephalo-thoracic trachea passes through the lower regions of the head, and

it receives air not only from the first spiracle, but also from the next two. Apart from these main tubes, the head is penetrated by a network of smaller tracheæ.

The tracheal system of the thorax is still more complicated, because the thorax contains many powerful muscles which must all have a sufficient supply of oxygen. It would be superfluous to describe the system in full; the main tracheæ are shown in Fig. 7, N, but it must be remembered that this figure represents a section of the body along the middle line, and many of the tubes that pass nearer the surface are not seen.

The tracheal system of the abdomen is considerably less complicated, and the tubes are more regularly distributed than in the thorax. Its main ramifications are as follows (Fig. 7, A, N): A pair of longitudinal, spiracular tracheæ (S), running along the ventral side of the abdomen, and connected by short branches with the spiracles. A pair of dorsal tracheæ (D) connected in each segment by transverse tubes with the spiracular tracheæ, but not connected with each other; they run parallel to each other along the sides of the alar muscles of the heart. A pair of ventral abdominal tracheæ (V), also connected with the spiracular tracheæ and with each other; they give off numerous branches to the nerve chain, while from their posterior portion some branches are emitted to the genital organs. Two pairs of alimentary tracheæ, upper (U) and lower (L), running along the alimentary tract and giving off numerous branches to it and to the genital organs.

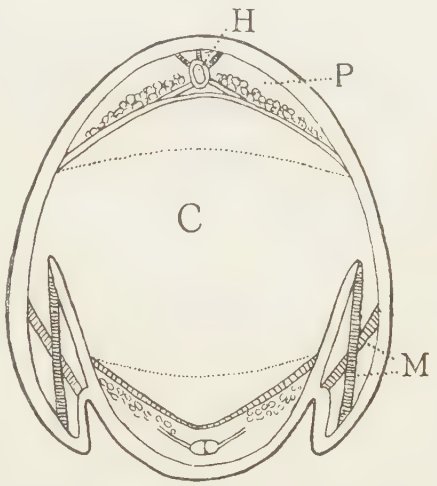

Fig. 8.—Diagrammatic transverse section of a grasshopper.—H, heart.—P, pericardial cavity.—C, central body cavity.—M, respiratory muscles (after Graber).

The system of *air-sacs*, which play so important a rôle in the bionomics of locusts in connection with migration (see next chapter), is in a close connection with the tracheal system, and the sacs themselves are but inflated sections of tracheal tubes. In the head there are a pair of fairly large sacs behind the eyes (CA), and several smaller ones in the region of the mouth-parts. In the thorax are situated a pair of the largest air-sacs (TA), and a pair of small ones connected with the metathoracic spiracles (M). In the abdomen there are eight pairs of large sacs, each of them representing a branch of the spiracular tracheæ; the sacs of each side are connected by a longitudinal tube running along the alimentary tract. These are the most important sacs, but it must be borne in mind that, apart from them, there are numerous smaller sacs and inflated sections of the tracheæ; in the head alone there are over 50 air-sacs (Packard, 1878).

As regards the process of *respiration*, we have some interesting, though

partly contradictory, data. Lee (1925) studied the problem on a number of North-American ACRIDIDÆ without finding appreciable differences. The respiratory movements consist of alternating expansion and contraction of the abdomen, and the respiration begins—contrary to what takes place in man—with the expiratory phase, when the active contraction of the abdomen expels air from the tracheal system (by means of special muscles, Fig. 8, M) ; the subsequent expansion of the abdomen, which must be due simply to its elasticity, not to the action of any muscles, causes an influx of air in the tracheæ (Regen, 1911). The ingenious experiments of Lee, by sealing certain groups of spiracles, have proved that all the spiracles do not function in the same way ; while the two pairs of the thoracic spiracles and the two first pairs of the abdominal ones serve only for inspiration, all the other abdominal spiracles are expiratory. Thus, when the abdomen contracts, the first four pairs of spiracles close automatically, and the air is expelled through the remaining abdominal spiracles ; when the abdomen expands, all the latter spiracles close and inspiration occurs through the first four pairs, the air entering from them into the spiracular tracheæ and then being driven through them into the other tubes (Lee).

FIG. 9.—The curve record of the respiratory movements, A, in an Acridid, D, in a Tettigoniid (after Regen).

Somewhat different views are expressed by Buisson (1925), who studied the respiratory processes in *Chorthippus*. According to him, the thoracic spiracles serve both for inspiration and expiration, while the abdominal ones are reserved for inspiration only. This author has, apparently, overlooked the possibility of different action in various pairs of the abdominal spiracles, and the experiments of Lee are perfectly convincing. Buisson stresses the rôle played by the air-sacs in the distribution of the air throughout the body.

Regen's interesting observations with a self-recording instrument have proved that expiration and inspiration follow each other very quickly, but that a pause then occurs so that respiration in the ACRIDIDÆ is intermittent (Fig. 9, A), not continuous as in the TETTIGONIIDÆ (long-horned grasshoppers ; Fig. 9, D).

The number of respiratory movements a minute depends closely on the temperature, light, and other stimuli, while it also differs according to the species and the sex. Particularly striking is the influence of temperature, as may be seen from the following table, showing the number of respiratory movements of a female of *Melanoplus femur-rubrum* at different temperatures (Lee, 1925) :

Temperature (C.).	Number of movements in a minute.
0°	0
9·5	5·8
11·0	7·5
15·0	9·7
16·6	11·0
19·5	15·0
22·0	18·1
24·0	20·8
25·5	26·0
26·6	26·6

Analogous results were obtained by Bodine (1921), who studied the amount of carbon dioxide given out in respiration. As a result of his experiments with more than 500 hoppers of different species, he obtained a curve of the average carbon dioxide output at different temperatures (Fig. 10).

The same author found that considerable differences exist in the carbon dioxide output in the different species and that hoppers give out more carbon

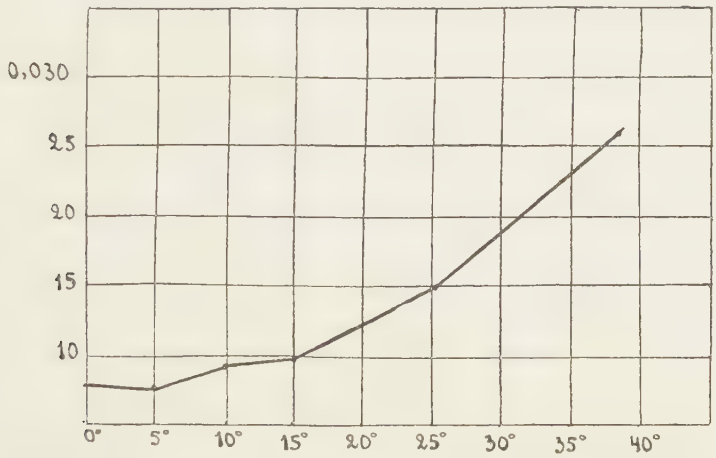

Fig. 10.—Carbon dioxide output of a grasshopper at different temperatures (after Bodine).

dioxide for each gram of their body weight than the adults, this indicating more active metabolic processes.

The expired air contains, according to the analyses of Lee, about 4 per cent. of carbon dioxide and about 16 per cent. oxygen.

As regards the more intimate physiological processes of respiration, we know very little. Thus it seems questionable whether the blood has any part in the transportation of gases within the body, as is the case with mammals; indeed, Bodine (1925*a*) is inclined to think, on the basis of determinations of the hydrogen ion concentration and oxidation tests of the blood of grasshoppers, that there are not sufficient data for attributing a respiratory function to their blood. Krogh (1913), who studied the composition of the air in the tracheal system of the hind leg of a grasshopper, found that the oxygen percentage is high during rest—up to 20 per cent., but after exhausting muscular exercise it is reduced to 5 per cent.; the percentage of carbon dioxide is always much lower than the oxygen deficit, and a large part of the carbon

dioxide formed in the tissues must be carried away by means other than the tracheæ.

When we consider that respiration may be taken as one of the best indicators of the activity of an animal, we have to acknowledge the necessity for a thorough research into the respiration of the ACRIDIDÆ, which might give us the key to many problems of their behaviour.

CIRCULATORY SYSTEM

The circulatory system of the ACRIDIDÆ is, as in all other insects, not closed, that is, it consists of a pulsating apparatus, or " heart," but there are no blood-vessels, and the blood circulates in the body cavity, reaching various organs from their exterior.

The body cavity is divided by two longitudinal septa in three parts (Fig. 8) : in the upper, or pericardial cavity (P), lies the *heart* (H), which is represented by a long tube fixed to the walls of the cavity by a series of paired muscles called alary muscles. The pericardial cavity communicates in front with the central cavity (C) surrounding the alimentary tract, while all three cavities also communicate behind. Apart from this, the pericardial cavity communicates with the central one by means of five pairs of openings placed symmetrically in five abdominal segments ; in each of these segments there is also a pair of openings in the walls of the heart itself through which it communicates with the pericardial cavity. Thus, in each segment there are a pair of openings through which the heart receives the blood from the pericardial cavity and another pair, through which the blood enters the latter from the central cavity. Through the last-named openings some Malpighian vessels enter into the cavity of the heart (Kovalevsky, 1894 ; also Graber, 1873, 1876).

A peculiar feature of the circulatory system of Orthoptera in general, including the ACRIDIDÆ, are the supplementary pulsating organs, *cephalic ampullae*, which are placed in the anterior part of the head, near the base of the antennæ, and, apparently, drive blood into them (Pawlowa, 1895).

The blood-corpuscles do not represent any peculiarities as compared with with other insects. Their shape varies considerably, even in the same individual ; thus in *Chorthippus* their diameter ranges from 0·012 to 0·0035 mm. In addition to the corpuscles, some isolated fat cells may be observed in the blood ; they are practically always round in shape, larger than the blood-corpuscles, and differ from them by their sharp outlines and by the dense central part resembling a nucleus (Graber, 1873).

It will thus be seen that, as with the respiratory system, our knowledge of the physiology of the circulation in the ACRIDIDÆ is practically nil.

EXCRETORY SYSTEM

The excretory system of the ACRIDIDÆ consists of the Malpighian tubes, fat body and phagocytic cells of the pericardial cavity.

The *Malpighian tubes* have some connection with the digestive system, and they are joined to the digestive tube at the beginning of the intestine

(Fig. 7, M). They look like fine threads, while their length, number, and arrangement differ in the various groups. In their function the Malpighian tubes are analogous with the kidneys of the higher animals and excrete uric acid and its derivatives.

The *fat-body* is a multilobate mass filling in the spaces between the various organs in the body cavity; while its shape is very complicated, it is not amorphous, though it appears to be so, and it is possible to establish its definite structure in each species (Buys, 1924). The fat-body plays a very important part in the physiology of the Acrididæ, but this part is still imperfectly known, and further investigations into its physiology should bring out many new facts and help to elucidate many of the outstanding problems of the biology of these insects. The excretory function of the fat-body consists mainly in the accumulation of urates, and this occurs only in individuals whose development has been retarded by some unfavourable external conditions (Pospelov, 1926); otherwise, the cells of the fat-body seem mainly to accumulate reserve materials which later serve for the development of the genital products. In accordance with this diversity of function of the fat-

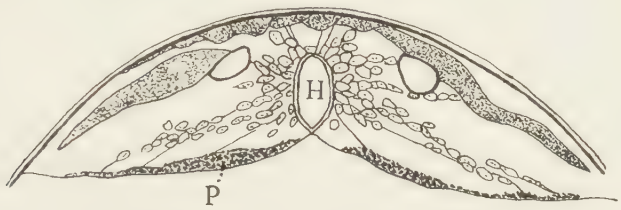

Fig. 11.—Cross-section of the pericardial cavity of *Calliptamus italicus*.—H, heart.—P, phagocytic cells (after Cuenot).

body during the different periods in the development of the insect and under different conditions, even its size, and still more its histological structure, undergo considerable changes; to this question, however, we will return later, when discussing the problem of locust migrations.

The *pericardial phagocytic organ* is represented by an accumulation of special cells along the pericardial membrane separating the pericardial cavity from the central body cavity (Fig. 11, P). In *Calliptamus italicus*, these cells are placed throughout the whole length of the membrane, while in *Acrida urrita* they are concentrated only in certain segments, particularly in the first abdominal ones. In their function the cells approach the free phagocytes of the blood, and they are able to envelop and to assimilate bacteria (Kovalevsky, 1894; Cuenot, 1895).

Reproductive System

The *male reproductive organs* (Fig. 12) include the unpaired testis, a pair of seminal ducts leading to the ejaculatory canal, a group of accessory glands, and the copulatory apparatus.

The testis (T) is situated near the dorsal surface of the abdomen. It is composed of a large number (up to 400 in *Locusta*) of slender

tubes, held together by connective tissue and covered from above by the fat-body; each of the seminal tubes, in which the development of the

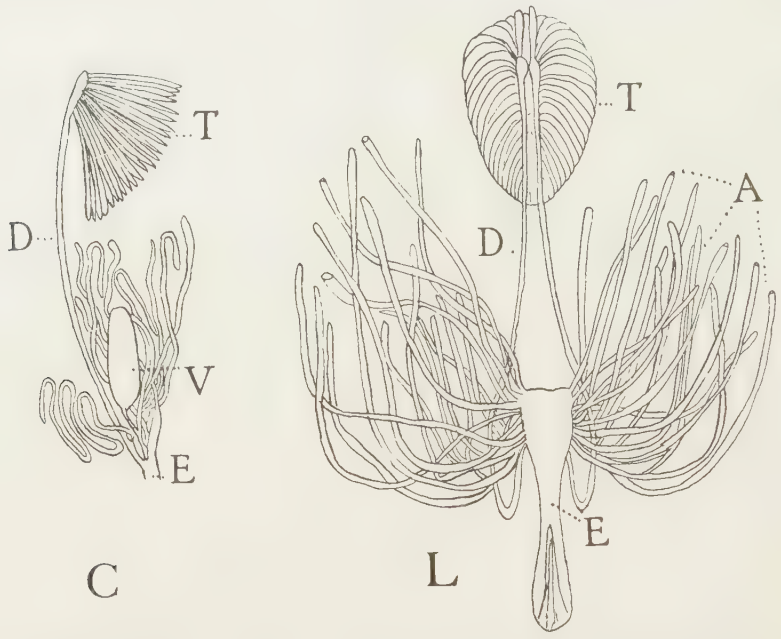

Fig. 12.—Male reproductive organs of Acrididæ.—L, *Locusta migratoria* (after Iwanowa).—C, *Calliptamus italicus* (after Dufour).—T, testis.—D, seminal duct.—E, ejaculatory duct.—A, accessory glands.—V, seminal vesicle.

spermatozoa (spermatogenesis) takes place, opens independently into the *seminal duct* (D). The latter are two in number; they run at first between the testis and the alimentary canal, but further back they encircle the latter and pass to the ventral side, where each of them opens separately into the *ejaculatory canal* (E). This canal is considerably broader than the seminal ducts, is lined by a chitinous cuticule and has muscles in its walls; it terminates in the *copulatory apparatus*. This is a somewhat complicated structure, consisting of several strongly chitinised parts. The main part is the *penis* (Fig. 13, P) to which is attached from above a pair of wing-like plates, the *upper genital valves* (U), and from below, a pair of *lower genital valves* (L); above the base of the whole organ there is placed a separate transverse plate, of very peculiar shape,

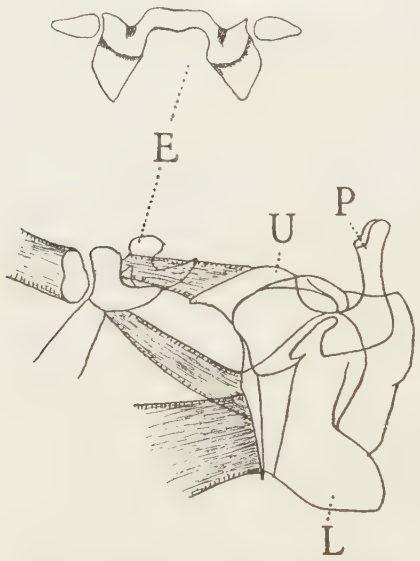

Fig. 13.—Male copulatory apparatus of *Anacridium aegyptium*.—E, epiphallus.—U, upper genital valves.—L, lower genital valves.—P, penis (after Chopard).

the *epiphallus* (E), which apparently plays an important part during copulation.

The accessory glands (Fig. 12, A) of the male genital apparatus are represented by numerous tubes, amongst which may be distinguished two or three kinds differing in colour, in histological structure and, probably, in function ; some are hyaline and excrete a mixture of albuminoids and lipoids, while others are white and their excretion is purely albuminoid (Ito, 1924) ; Iwanowa (1926) refers to a third type of accessory glands, a pair of long milk-white tubes covered by the fat-body of bright orange colour, but these tubes must be the paired *seminal vesicles*, which in some ACRIDIDÆ are not like tubes (Fig. 12, A, V). The function of the accessory glands is connected with the formation of spermatophores (see below).

The *female reproductive organs* consist of paired ovaries, oviducts, vagina, spermatheca, and accessory glands.

The *ovaries* (Fig. 14, O) consist each of a large number of egg-tubes, in which development of eggs (vogenesis) takes place. In the sexually mature females the ovaries occupy a very large portion of the body cavity and attract immediate attention on dissection. Each of the egg-tubes opens independently into the wide *oviduct* (D), and the two oviducts join together to form the *vagina* (V), which opens to the exterior at the base of the subgenital plate. The upper end of each oviduct extends beyond the group of the egg-tubes in the shape of a blind appendix, the *accessory gland*, which excretes an albuminoid substance (not chitin) that serves for the formation of the egg-capsule. A special appendage of the female genital apparatus is the *spermatheca* (S), which is a sinuous tube opening independently between the lower valves of the ovipositor, that is, close to the opening of the vagina ; at its other, inner, end the spermatheca is often expanded and forms a *seminal vesicle* (SV) (for literature on the genital system, see Chopard, 1921 ; Ito, 1924 ; Harman, 1925 ; Fedorov, 1927 ; Sokolow, 1925 ; Iwanowa, 1926).

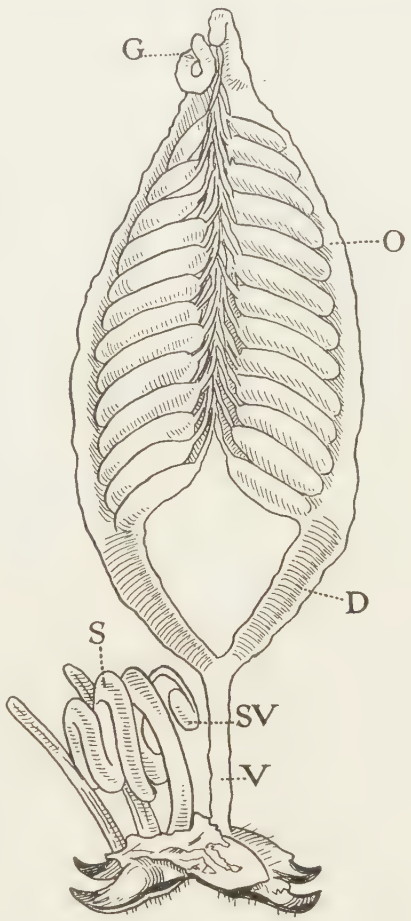

FIG. 14.—Female reproductive system of *Locusta migratoria*.—O, ovaries.—G, accessory glands.—D, oviduct.—S, spermatheca.—SV, seminal vesicle.—V, vagina (after Pospelov).

Nervous System

The *central nervous system* of the Acrididæ is represented by *ganglia* connected with each other by commissures and forming a chain along the

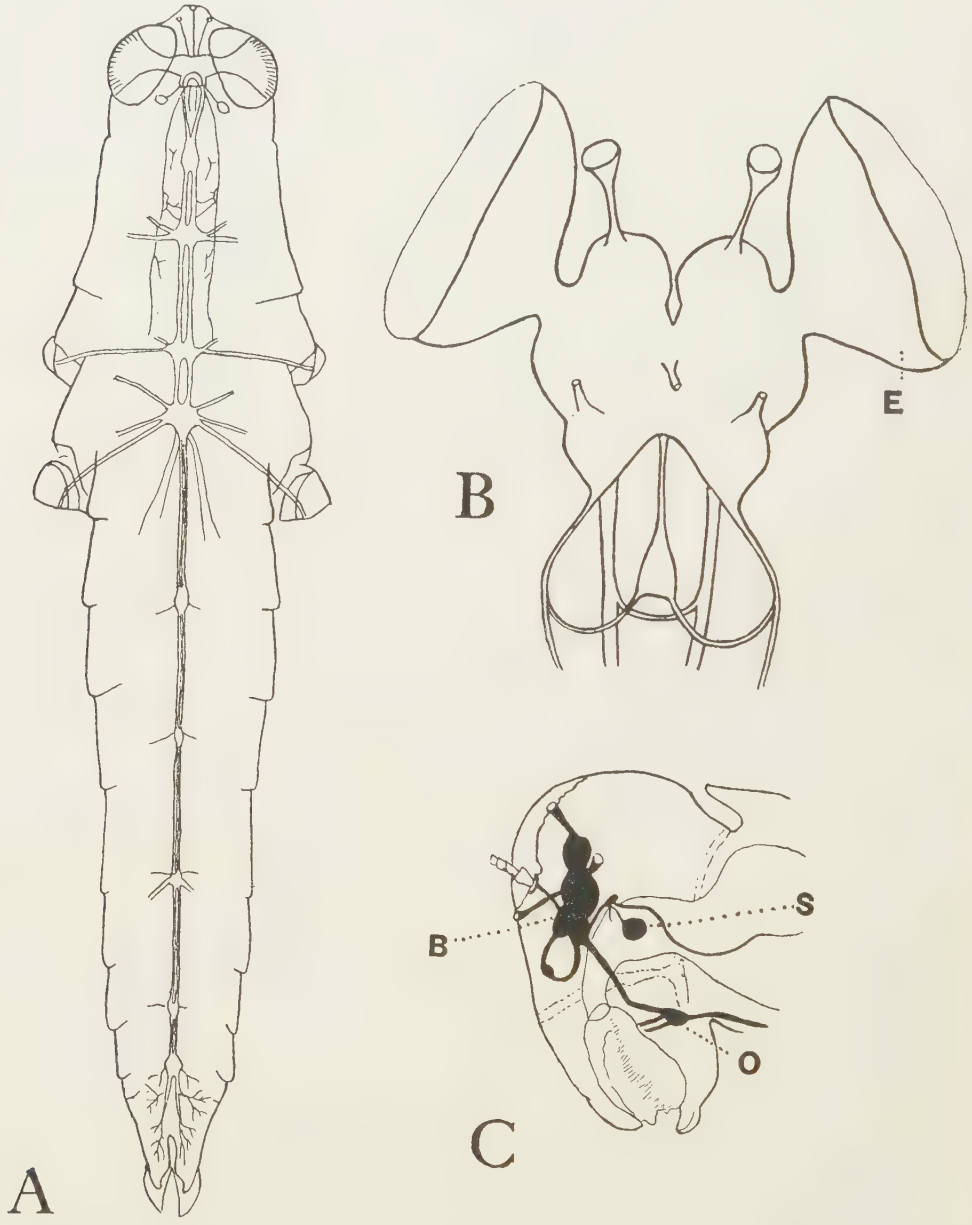

Fig. 15.—Nervous system of a grasshopper.—A, ventral nervous chain.—B, cephalic ganglion (brain).—O, sub-œsophageal ganglion.—S, sympathetic nervous system.—E, optical lobes of the brain (after Packard).

ventral side of the body cavity. The total length of the nerve chain usually exceeds that of the body, owing to its not being straight.

More complicated than the others is the *cephalic ganglion*, or brain (Fig. 15, B), which sends off nerves to the sense organs and is situated in the head above the œsophagus. A pair of commissures runs backwards from it, encircles the œsophagus and joins the *sub-oesophageal ganglion* (O), which gives off nerves to the mouth-parts. From this ganglion arises the ventral nervous chain (Fig. 15, A), which consists of paired, in places fused, commissures and ganglia—three thoracic (one in each of the thoracic segments) and five abdominal, the last of which is considerably larger than the others and emits nerves to the genital organs.

Very detailed information on the anatomy of the brain has been given in a paper by Viallanes (1887), and I will not repeat it here since the functions of various sections of the brain are practically unknown. The only work known to me in which the functions of various ganglia are discussed (Ewing, 1904) is based on experiments with removing or destroying certain ganglia. Their results may be briefly summarised as follows :

1. The cephalic ganglion is a centre directing swallowing movements and controlling reflex ones. A grasshopper with this ganglion removed cannot move its mandibles or swallow food, but it reacts to all external stimuli by exaggerated movements, jumping or flying off ; very typical are the incessant movements of the palpi and the rhythmical movements of legs in the absence of any stimulus.

2. In the co-ordination of movements the cephalic ganglion takes no part ; without it, but under the influence of external stimuli, the insect can walk, jump, fly, and keep its normal balance ; the respiratory movements of the abdomen of such insects remain normal.

3. The hind portion of the cephalic ganglion is a controlling centre for the anterior portion, which is a centre for voluntary movements ; if the hind portion is destroyed, the insect moves incessantly ; on the contrary, if the whole ganglion is destroyed, movement in a given direction ceases altogether.

4. Each of the thoracic and abdominal ganglia represents an independent centre for respiratory movements and reflexes of the respective segment and its appendages.

5. The sub-œsophageal ganglion plays some part in the preservation of balance during movement.

These data of course are very far from being complete, and extensive experimental research on the functions of the nervous system is urgently wanted, since only on this basis would it be possible to study the important problem of the behaviour of locusts and grasshoppers (see Chapter IV).

The *sympathetic nervous system* (Fig. 15, S) connected with the main system, consists of the cephalic sympathetic ganglion placed above the œsophagus, the œsophageal ganglion and of three paired ganglia. The nerves coming from all these ganglia control digestion and the movements of the heart and the muscles of the spiracles (for details, see Bordas, 1900 ; Pierantoni, 1900, describes the sympathetic system of *Locusta*, and in another paper, 1902, he gives information on its histology).

Organs of Vision

For purposes of vision the Acrididæ have simple eyes, or ocelli, and compound ones (Fig. 16).

The *ocelli* are normally three in number. One, an unpaired frontal ocellus, is situated on the frontal ridge about its centre, while a pair of lateral ocelli (O) is placed at the inner margins of the compound eyes, usually quite close to them. In some Acrididæ the frontal ocellus is very feebly developed and may even disappear altogether ; this is usually found in the wingless species, while in all good fliers the ocelli are well developed.

The *compound*, or *facetted*, *eyes* (E) are always well developed, oval or round in shape, and situated on the side of the head, so that their field of vision extends not only forwards but sideways.

I will not here describe the anatomical and histological details of structure of either kind of eye since they do not differ in any important respect from those of other insects (see Link, 1909 ; Jorschke, 1914).

Fig. 16.—Horizontal section through the head of a grasshopper.—O, lateral ocellus.—E, compound eye.—L, optical lobe of the brain (after Link).

As regards the functions of the eyes and the ocelli, practically nothing can be said, apart from some general considerations, because no systematic investigations on the vision of the Acrididæ have been ever undertaken, and it remains uncertain whether they can differentiate colours, see the shape of objects, or only their movements, etc., to say nothing of the respective functions of the eyes and the ocelli. According to Demoll and Scheuring (1912), the ocelli in insects generally serve to determine the distance from objects, and they function normally only if the compound eyes are present ; if, however, the latter are removed, or covered with paint, the insect behaves as if blind, which indicates that the ocelli require a stimulus from the compound eyes.

The importance of exact investigations into the vision in these insects will be fully realised in connection with their behaviour (see Chapter IV), and it is to be hoped that this important problem will be taken up by investigators.

Organs of Chemical Perception

This group comprises organs of smell, *i.e.* of reception of chemical stimuli through the air, and organs of taste, or reception of similar stimuli by

immediate contact. An exact knowledge of both must, obviously, be very important for understanding certain aspects of the bionomics of ACRIDIDÆ, while its practical importance is particularly great in connection with the control measures based on these senses (poisoned baits). It is therefore very regrettable that our present knowledge of this problem is not only fragmentary, but extremely vague.

As regards the *sense of smell*, it has nearly always been supposed to be located in the antennæ, though there is still little evidence in favour of this. Röhler (1905) made particularly detailed studies of the organs of sense situated in the antennæ of *Acrida turrita*, a common South European species. According to him, there are nerve endings of three different types on the antennæ of this insect ; long, fine, strongly chitinised bristles on the first to eighth joints, but most numerous on the third ; short spines (Fig. 17, S) on all joints, but more numerous on the middle ones ; and pits with a flask-shaped organ at the bottom (Fig. 17, P), which may be found on the 3rd–17th joints, but more

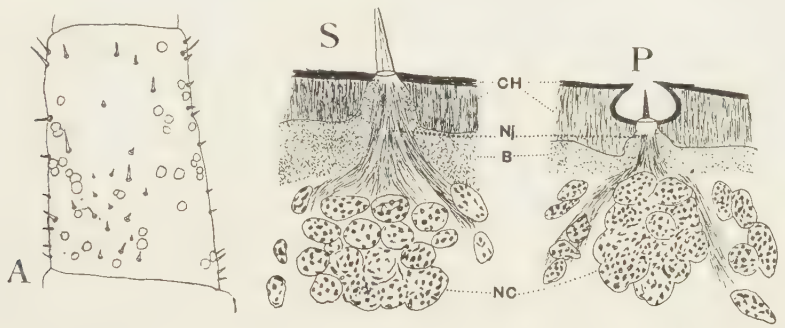

FIG. 17.—Antennal sensory organs of *Acrida turrita*.—A, one of the middle antennal joints.—S, sensory spine.—P, sensory pit.—CH, chitin.—N, nerve filaments.—B, basal membrane.—NC, nerve cells (after Röhler).

densely placed on the 10th–17th. The average number of each kind on one antenna was found to be : in the males, 77 bristles, 3738 spines, and 1718 pits ; in the females, 83 bristles, 2330 spines, and 1362 pits.

Based only on the histological structure of these organs, Röhler came to the conclusion that the bristles and spines must be organs of touch ; the largest of the spines he thought served for the reception of stronger stimuli by direct contact, while the finer ones may serve to appreciate movements of the air, as for instance, during flight. The pits he considered to be organs of smell, but again only because from their histological structure they seem to be unsuitable for any other purpose. A collateral proof in support of this view Röhler found in the fact that the males have a larger number of pits than the females, but his experiments were not completed.

McIndoo (1920), who studied the organs of smell in nearly all groups of insects, points out that Röhler's assignment of this function to the antennal pits cannot be accepted, because there is present in them a dense chitinous covering that precludes direct contact between the air and the nerve endings ;

Röhler, though admitting this, thinks that the perception of odours is possible by means of diffusion of gases through chitin.

McIndoo himself is inclined to regard the so-called *olfactory pores* as organs of smell in Orthoptera generally. These have been found by this author in eight different species of grasshoppers (all those studied), and in both sexes, and in one species in all the larval stages as well. These pores occur on the legs, antennæ, elytra, wings, abdominal segments, mouth-parts, cerci, and the ovipositor. In order to give an idea of the distribution of pores and its variation according to the sex and the stages of development, I give the following extracts from the tables of McIndoo, relating to one species :

	Mouth-parts.	Head capsule.	Antennæ.	Abdominal segments.	Cerci.	Ovipositor.	Legs.	Elytra.	Wings.	Total.
I stage ..	272	9	22	54	3	—	367	—	—	727
II stage ..	276	11	28	45	4	—	429	—	—	793
III stage ..	279	9	42	54	3	—	449	—	—	836
IV stage ..	344	14	56	50	5	—	485	—	—	954
V stage ..	467	7	98	45	—	53	660	84	66	1480
Adult female ..	520	5	106	45	—	55	718	84	33	1566
Adult male ..	482	7	110	36	—	—	720	86	30	1471

It will be seen from this table that the total number of the pores increases with the successive moults, and that on the cerci only do they disappear in the last larval stage.

The number of pores and their distribution in other species of grasshoppers studied by the same author do not differ very much from the example given ; the total number varies from 727 to 1616.

In structure the olfactory pores are small openings in the chitin surrounded by a ring-like wall of raised chitin and leading into a canal of larger diameter, where a nerve from the corresponding nervous end-cell comes into contact with the air (Fig. 18).

Fig. 18.—" Olfactory pores " of a grasshopper.—A, surface view of a group of pores.—B, section of pores (after McIndoo).

The olfactory function of these pores (found by McIndoo in all other insects, though differing somewhat in structure) lacks proof just as much as the case of the antennal organs of Röhler. McIndoo, however, quotes some experiments of his, which at least prove that the antennæ cannot be considered the only part of the body where the organs of smell are concentrated. The experiments were made first with normal grasshoppers which were offered various aromatic substances, and their reactions towards them, in the shape of certain kinds of movements, were noted. The same individuals were then subjected to the operation of cutting off the antennæ at the base of the third joint, and the same experiments with

aromatic substances were repeated ; the results showed that, on the average, the normal grasshoppers reacted after 9 seconds and the mutilated ones after 8·4 seconds, there being practically no difference in the reception of smell when the antennæ were cut off. The mutilated insects were kept under observation and led a perfectly normal life in all respects ; they ate, drank, paired, and lived just as long as normal ones.

If these experiments prove (though still not quite definitely) that the antennæ have no olfactory function, they do not prove that this function is situated in the pores. McIndoo sees the main support for his view in the fact that the pores are better adapted by their anatomical structure for the reception of chemical stimuli than are the antennal organs of Röhler, since the nerve in the pores comes into direct contact with the air. The distribution of the pores all over the body makes experimental proof of their function practically impossible, and our knowledge of the organs and the sense of smell remains in a very unsatisfactory condition.

As regards the *organs of taste*, it is natural to look for them in the mouth-parts, and Nagel (1894) ascribes this function to the pits with flask-like organs at the bottom of them that occur in numbers on the mouth-parts. Kulagin (1922) pointed out that their number decreases with the development of the larva. Their function may be only guessed at on the basis of their structure and position.

Tympanal Organs

The so-called tympanal organs, situated on the sides of the first abdominal segment (Fig. 1, TO), were first described by De Geer in 1804, and since then they have been most thoroughly studied by Graber (1876, 1882), Schwabe (1906), and many other authors.

The tympanal organs are not present in all Acrididæ, but in the great majority of them, being undeveloped, or, rather, degraded, only in some, mainly apterous species. The exterior view of a tympanal organ varies somewhat ; in certain species it is represented by an oval membrane, which is either level with the surface of the abdominal segment or lies in a depression, and is encircled by a raised chitinous ring ; in others the ring forms a shell-like cover above the membrane ; in still others the development goes further and the whole membrane becomes invisible, while a narrow slit leads into the cavity between the shell and the membrane.

The membrane of the tympanal organ (Fig. 19, M) is formed by a modification of the skin ; it is very elastic and strong. Its outer surface is covered with minute spinules forming regular rows and becoming larger as it nears the front margin. At the latter the spiracle (Sp) is placed, and approximately in the centre of the membrane (a little nearer to the front margin) on its inner side is situated a special, somewhat complicated organ composed of several parts, as follows : (1) folded body (F), a fold of the membrane covering the nervous end-apparatus ; (2) styliform body (St), a thickening of the chitin of the membrane ; and (3) pyriform body (P), a sharply outlined

pear-shaped chitinous structure. These bodies are connected with the end-apparatus, called *Müller's organ* (MO), of a special nerve (N). A strong appendage (MU) of the chitinous frame of the membrane at the front of its lower margin serves for the attachment of a muscle ; another, smaller muscle is affixed to the membrane near its hind margin (the muscles are not shown in the figure). Under the membrane there lies a large air-sac communicating with the outer air through the spiracle mentioned above ; the air-sacs of the second abdominal segment also lie very close to the membrane.

Such is the structure of the tympanal organ in its main features ; the details vary somewhat in different species, but the general plan remains essentially the same (for detailed descriptions of the anatomy, as well as the histology of the tympanal organs, see papers by Graber and Schwabe). While, however, its structure has been thoroughly studied, our knowledge of its functions is very vague. The general principle of its structure leads naturally to the suggestion that it is an organ of hearing. This is also supported by a study of the histological structure of the nerve endings in Müller's organ as well as by the fact that the tympanal organs are, as a rule, absent or reduced in the species in which there are no sound-producing organs. Nevertheless, the experimental data, which would decide the problem definitely, are lacking, while there is an indirect indication that the tympanal organs are, at any rate, not the only ones for the reception of sound, since in Rudow's (1870) experiments female grasshoppers with the tympanal organs perforated, or covered with wax, reacted like normal females to the stridulation of males by moving their antennæ in the direction of the sound. Observations by Vayssière (1921 ; see Chapter IV) show that the tympanal organs may serve for the reception not only of sounds but of other vibrations of the air as well. Finally, Schwabe (1906) has found in the tympanal organs nerve endings that do not differ in their structure from the olfactory ones.

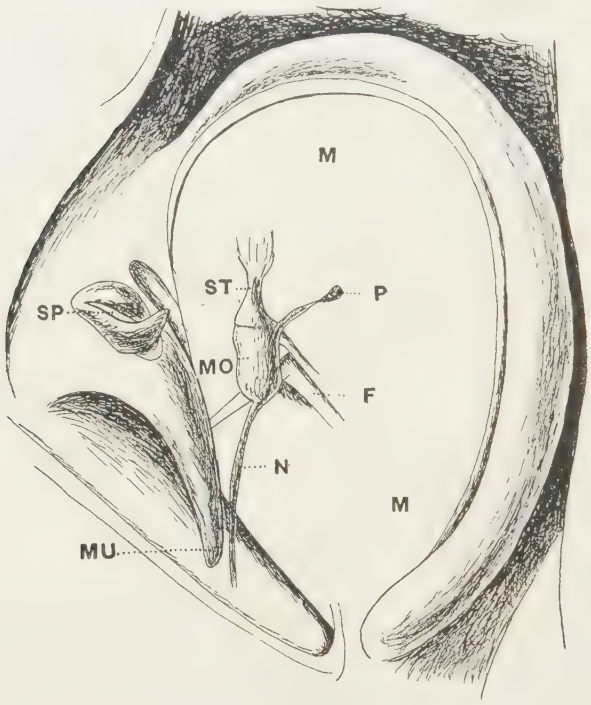

Fig. 19.—Inner view of the tympanal organ—M, membrane.—Sp, spiracle.—MO, Müller's organ.—St, styliform body.—P, pyriform body.—F, folded body.—N, nerve.—MU, chitinous appendage for the muscle (after Schwabe).

The unquestionable importance of the tympanal organs in the behaviour of the ACRIDIDÆ makes detailed experimental studies of their function vitally necessary. Experiments of this kind should not present great difficulties, and their results might help to solve certain problems in the behaviour of these insects that are of immediate practical interest.

SOUND-PRODUCING ORGANS

According to popular opinion, stridulation is a distinctive character common to all ACRIDIDÆ. This is, however, not precisely the case, although the majority of species are able to produce sounds and possess special organs, which may be of several different types.

The type of stridulating organ that is most commonly found is based on the principle of friction of the hind femur against the elytra. On the inner surface of the femur may be seen with a hand lens a slightly raised ridge (Fig. 20, P), which is sometimes serrated or consists of a series of separate tubercles. Under the microscope this ridge is seen to consist of a row of more

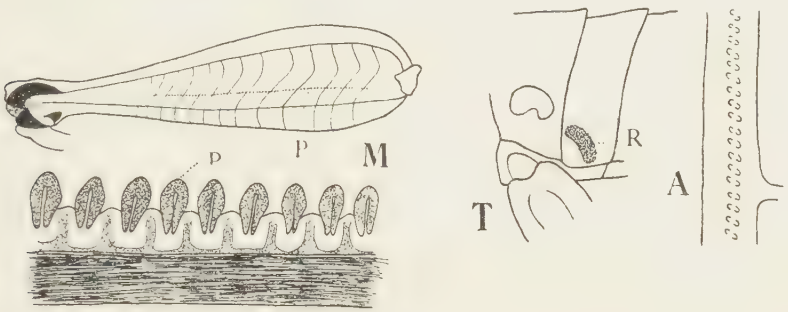

FIG. 20.—Sound-producing organs of various grasshoppers.—M, *Mecostethus grossus*.—P, pegs.—A, discoidal vein of *Aiolopus* (after Petrunkewitch and Guaita).—T, *Tmethis*, base of abdomen.—R, rough plate (original).

or less numerous pegs (P). When the femur is rubbed against one of the veins of the elytra (usually the radial or the discoidal), the pegs catch on the vein, and this results in the vibration of the elytra, producing a sound that is increased by the resonance of the expanded elytral fields.

In some ACRIDIDÆ there are no pegs, only a raised ridge, and in this case the vibration is produced because the vein, against which the femur is rubbed, is itself serrated. Sometimes even the raised line disappears, and the friction apparently takes place between the usual lower inner keel of the femur and an elytral vein ; in such cases (*Hilethera*, *Aiolopus*, Fig. 20, A) the discoidal vein of the elytra is very strongly serrate. In another case (*Brachycrotaphus*) there are very strongly developed pegs on the femur, and in addition the spines of the inner side of the hind tibiæ are expanded and provided with closely placed transverse ridges, which seem also to take part in the stridulation.

The arrangement of the pegs as well as their shape and number vary in different species ; they may form an irregular or a regular row ; they may

be placed either very close to each other or be widely separated. Their number and their density of distribution must naturally affect the pitch of the sound, altering the number of vibrations produced in a second ; further modifications of the sound may be caused by the rapidity of movements of the leg and by the relative development in various species of the resounding elytral fields. As examples, it may be pointed out that in *Arcyptera microptera* there are about 60 pegs, in *Gomphocerus sibiricus* 150, and in *Stenobothrus lineatus* over 200 (Graber, 1871). Apart from such specific differences, there is also a sexual dimorphism, the females, as a rule, possessing fewer or smaller pegs than the males ; in certain cases the pegs in the female represent a structure transitory to the hairs, proving that they originated as modifications of hairs (Cobelli, 1886 ; Graber, 1871 ; Petrunkewitch and Guaita, 1901).

The pitch of the stridulation, its length and the " tune " are undoubtedly specific ; this has been proved by a few attempts at expressing, by means of musical signs, the stridulation of various species (Scudder, 1868 ; Yersin,

Fig. 21.—Stridulation of grasshoppers.—S, *Gomphocerus sibiricus*.—*b*, *Chorthippus biguttulus*.—*c*, *C. bicolor*.—*m*, *C. mollis*.—An empty oval means a sound lasting 4–5 secs. ; ditto, with a vertical tail, 2–3 secs. ; black oval, 1 sec. ; ditto, with a flag, less than ½ sec. ; ditto, with a treble flag, single beats following each other too rapidly to be counted (after Yersin).

1854 ; Fig. 21). The stridulation also varies in the sexes as well as with the external and internal conditions. Thus, the pitch is raised apparently by a rise in the temperature, while the males produce special " tunes " and tones at the time of pairing.

It may be suggested that stridulation is only an external evidence of increased physiological, particularly sexual, activity. It remains obscure whether stridulation has any significance during pairing as a means for attracting the opposite sex ; this is the explanation usually suggested, but without much reason, since we do not yet know whether the sounds are heard by the insects themselves.

Another type of sound-producing apparatus, much less perfect and capable only of producing feeble and indefinite sounds, may be found in the desert grasshoppers of the genus *Tmethis*. They possess on the second tergite, at its lower margin, a rough plate (Fig. 20, R), and another similar plate on the corresponding place on the inner surface of the femur ; rubbing the two plates against each other produces a feeble sound.

A considerable development of the same method may be observed in the peculiar South African grasshoppers of the subfamily PNEUMORINÆ, in which there are a series of ridges on the sides of the abdomen, while the latter in the male is enormously inflated and acts as a resounding apparatus.

Many of the ACRIDIDÆ are capable of producing during flight sounds resembling those of a rattle. As examples may be quoted *Psophus stridulus*, *Chorthippus scalaris*, various species of *Bryodema*, *Dissosteira*, etc., and an examination of all them reveals that they all possess one character in common, this being the strongly thickened main veins of the hind wings. The principle on which the sound is produced is not very clear, but Karny (1908) has shown that only the hind wings are used in making it, since it does not lose its volume if the elytra are removed. It may be suggested that the sound results from the fan-like closing and opening of the wing during flight; there is no need for the wing to close altogether (this does not happen), as the sound may be produced by partial slackening of the membrane between the veins and the subsequent sudden expansion. Sounds of this kind are produced almost exclusively by the males, and in some species (*Bryodema*, *Dissosteira*) the males rise in the air and circle for some time as if for the special purpose of producing them; the suggestion that this is done in order to attract the females is without sufficient foundation, and it is more likely that it is merely an expression of physiological excitation.

CHAPTER III

DEVELOPMENT AND TRANSFORMATIONS

The Egg and the Development of the Embryo

Structure of the Egg.—The eggs of the Acrididæ are relatively large and have the shape of an elongated, slightly bent, cylinder with rounded ends (Fig. 22). Of an aberrant type are the eggs of the Tetrigidæ in which the upper end is elongated into an appendage (Fig. 23 ; Hancock, 1902).

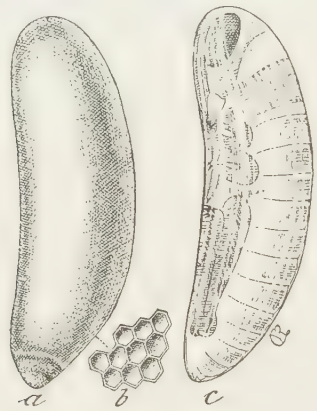

Fig. 22.—Egg of *Melanoplus spretus : a*, covered with chorion ; *b*, portion of chorion enlarged ; *c*, egg before hatching with the chorion peeled off and the embryo visible (after Riley).

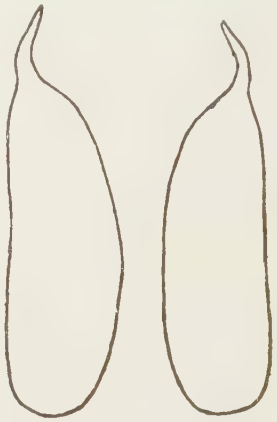

Fig. 23.—Eggs of a Tetrigid (after Hancock).

The egg has two coverings, an outer which is opaque and called the *chorion*, and an inner which is transparent and called the *vitelline membrane*. The chorion for some time after the egg has been laid adheres to it rather firmly

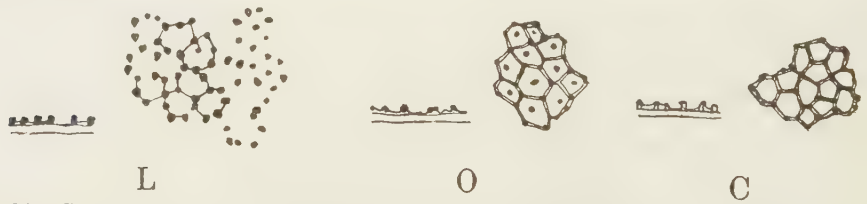

Fig. 24.—Structure of chorion in the eggs of L, *Locusta migratoria ;* O, *Oedaleus decorus ;* C, *Calliptamus italicus* (after Plotnikov).

and is whitish in colour, but later it becomes yellowish, then brownish and brittle, and peels off in patches. When examined under a microscope, the chorion of the eggs of many Acrididæ has a peculiar sculpture, formed by crossed ridges, tubercles, or small spines, etc. (Fig. 24). This suggests that a

study of the sculpture of the eggs might be of considerable importance for their identification (Plotnikov, 1912, 1926), but very little work has been done on these lines, and its actual value for systematic purposes is uncertain.

The vitelline membrane has no structure ; it is very strong and elastic and able to withstand considerable pressure as its function is to protect the egg from mechanical influences such as pressure and from desiccation. Beneath this membrane there is a layer of protoplasm, which represents the actual living part of the egg, and under it again lies the yolk, *i.e.* the reserve substance that serves to build up the embryo.

At one end of the egg (the upper one, when the egg is in the normal position in the ovary of the female or in the egg-pod), there is a small tubercle of a darker colour, with numerous very fine pores in it, through which the spermatozoa enter the egg during fertilisation ; this group of pores corresponds to the so-called micropyle in the chorion of the eggs of other animals.

The eggs in the ovaries are arranged in a definite order ; they are in slightly inclined rows, each egg having its concave side downwards and forwards, this side being parallel to the ventral surface of the female. The end of the egg bearing the micropyle is directed downwards and backwards, and the same position is preserved when the egg is in the egg-mass.

The Development of the Embryo.—After the egg has been fertilised (or in the absence of fertilisation ; see below), the development of the embryo begins. The embryo appears first at the ventral side of the egg and is directed with its head to the hind lower end of the latter ; as development progresses, however, the embryo gradually shifts backwards along the ventral side of the egg, turns round its hinder end and begins to grow along the dorsal side of the egg so that the fully formed embryo lies parallel to the body of the female with its head directed forward. This turning of the embryo apparently occurs in most of the Acrididæ in the egg-pod, and the embryos ready for emergence thus lie with their head upwards, which must facilitate that act. The phenomenon of the turning of the embryo (or, at least, its various phases) is easy to observe because the eyes are large and dark and can be easily seen through the membrane of the egg after the chorion has been carefully removed. Observations of this kind are of considerable practical importance, since the position of the embryo and the degree of its development give an indication when the emergence of the larvæ may be expected. In order to get the embryo out of the egg, Plotnikov (1912) recommends cutting off the anterior end and then pressing the egg with the fingers beginning from its hind end ; the embryo then comes out entire, and when placed in a dish, is easily separated from the yolk by means of a jet of water.

Simultaneously with the development of the embryo and in obvious connection with it, some changes occur in the external appearance of the egg. It increases in size, especially in diameter ; thus, in the Moroccan locust the average length of an egg soon after it has been deposited is 5 mm., and its diameter 1–1·2 mm., while before hatching the length increases to 5–6 mm., and the diameter to 1·5–2 mm. (La Baume, 1918). This swelling of the egg causes the chorion to crack and to peel off. At the cephalic end, *i.e.* the

upper end of the egg when it is in the normal position in the egg-pod, the large eyes become very noticeable even through the chorion.

The estimation of the *period necessary for the development of the embryo* is of great practical interest, but the problem has as yet been very insufficiently studied.

The simplest case should occur in some tropical species, in which this period may be expected to be the shortest. According to Vosseler (1905), the eggs of *Schistocerca gregaria* in East Africa require not less than 15–16 days for their development, but very often hatching is retarded for several days, mainly because of the dryness of the ground (see below regarding the rôle of humidity). In the Mexican *Schistocerca paranensis*, the incubation period lasts from 14 to 75 days according to the local and the seasonal conditions (Dampf, 1925). In the temperate climate of Turkestan, Plotnikov (1915) found the period of the development of the eggs of *Locusta migratoria* ph. *danica* to occupy 16–30 days, while for the Egyptian grasshopper (*Anacridium aegyptium*) in the South of France this occupies several weeks (Grassé, 1913).

These data and others of the same kind throw very little light on the important question as to the actual factors that determine the length of the incubation period. Theoretically it seems clear that the most important must be the *temperature*, and some attempts to calculate its influence may be found in the reports of the United States Entomological Commission (1878). The essence of the data collected by this Commission is that the process of development takes place only when the temperature is above a certain minimum. This critical point has been taken as 50° F. (10° C.), and the determinations of the time required for development may be based on the number of hours during which the temperature is above the critical point, as compared with the number of hours necessary for complete development at 60° F. (15·5° C.), which has been found empirically to be 1440. These calculations are, however, founded on observations under field conditions and by very imperfect methods, while the minimum temperature was apparently estimated too low.

Much more exact data are given in a recent paper by Bodine (1926) which presents the results of a very long series of experiments under laboratory conditions and with a careful valuation of all factors. The critical point or *developmental zero* has been determined by that author (not by direct experiments, however, but by calculation from the data on the period of development at higher temperatures) as 18° C., that is, considerably higher than that accepted by the Entomological Commission.

The following figures of the length of the incubation period at different temperatures (kept constant during the whole of a given experiment) were obtained for several species :

Species.	Length of incubation period (days).	
	23° C.	30° C.
Melanoplus differentialis	89	28
Melanoplus femur-rubrum	45	14
Chorthophaga viridifasciata	53	19
Dichromorpha viridis	86	—
Rhomalea microptera	150	—

It will be seen from this table that the amount of heat required by different species for incubation is very unequal, while for each species there is a well-defined inverse proportion between the temperature and the length of the incubation period. This is still more strikingly demonstrated in the following table of observations on a single species, *Melanoplus differentialis:*

Temperature (C.).	Incubation period (days).	Coefficient of development in a day.
36·0	28·00	0·0357
30·0	47·69	0·0209
26·6	69·59	0·0145
23·0	89·00	0·0112
20·0	106·60	0·0093

The last column is obtained by dividing one by the number of days of the incubation period, and shows therefore by what fraction of the complete development the embryo advances in one day. The sharp increase in the coefficient of development at the higher temperatures demonstrates most

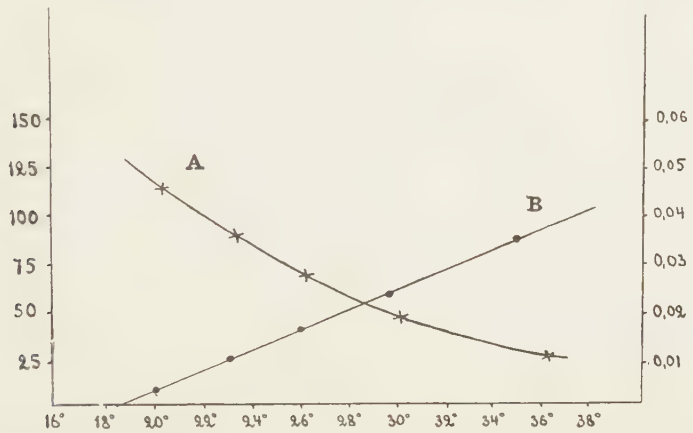

FIG. 25.—The length of incubation period at different temperatures. Number of days on the left; coefficient of development on the right.—A, curve of development at various temperatures; B, line of velocities (after Bodine).

clearly the acceleration of the incubation process that a rise in temperature causes. The diagram based on the data of the last table (Fig. 25, A) shows that after several points of the curve of development corresponding to certain constant temperatures have been determined, it is possible to calculate theoretically the length of the incubation period at any given temperature, *i.e.* to predict the date of hatching with great precision. In the laboratory of the University of Pennsylvania where Bodine worked, this method is actually applied in order to obtain freshly hatched larvæ exactly when they are wanted. The curve of development is a hyperbole; in connection with it, it is useful to trace the line of velocities or of the coefficients of development at different temperatures (Fig. 25, B), by marking on the right ordinate the coefficients for the observed temperatures; this line is always straight, and the point where it crosses the abscissa, on which the temperatures are plotted, corresponds to the critical point or developmental zero, which latter can be always found in this way.

All these data refer to laboratory experiments at a constant temperature, which does not happen in nature, but they supply some useful hints as to the rôle of temperature in the development of the eggs generally. For the ACRIDIDÆ of temperate regions, it must be a fact of importance that hibernation usually occurs in the egg stage, which is thus exposed to low temperatures. These temperatures in themselves are not particularly injurious to the eggs, since those of the ACRIDIDÆ are able to withstand complete freezing and subsequent thawing without any ill effects. Moreover, the experiments by Bodine have revealed the very interesting point that eggs subjected to the action of a low temperature develop, on raising it above the developmental zero, much more rapidly than those that have been all the time under the influence of a high temperature. Thus, for instance, the eggs of *Melanoplus femur-rubrum* at a constant temperature of 23° C. develop in 45 days, with a coefficient of 0·022, but if they have been kept in the open air for 39 days and then subjected to a constant temperature of 23° C., their development is completed in 40 days, with a coefficient of 0·025. In a series of other experiments the acceleration of development after exposure to a low temperature was still more pronounced, and in some cases development was half as rapid again as compared with the normal for the corresponding constant temperature.

Thus, a low temperature, though it interrupts the development of the embryo, also acts as a stimulus that accelerates development as soon as its influence is removed. For some species, a temporary cooling even seems to be a condition necessary for normal development, and eggs kept at a constant high temperature from the time of oviposition fail to develop (Carothers, 1923). The stimulating action of low temperatures according to Bodine (*l.c.*) differs in its effect according to the stage of the embryo when cooling took place. If the eggs are kept at a constant temperature of 10° C. from the moment of laying, the subsequent raising of temperature does not result in an acceleration of development ; if, however, they are first kept at a temperature above the developmental zero, then cooled, then again warmed, the acceleration in development is marked. The initial action of high temperature must be not too prolonged, or else there will be again no acceleration. This means that low temperatures produce an acceleration in the development of the embryo only when it was subjected to their action at a definite stage of its development. What that stage is is unknown.

In nature the following is the course of events in most of the ACRIDIDÆ. Development begins shortly after the eggs are laid ; it is then interrupted and resumed again only next spring, when the temperature after the winter cooling rises above the developmental zero. This interruption of development, or *embryonic diapause*, could apparently be explained simply by the deterrent action of the low winter temperatures, but this is not so, since in many species of temperate regions oviposition takes place quite early in the autumn (or even in summer), and the diapause begins when temperatures are well above the zero of development. Also attempts to break the diapause in the laboratory and to make the eggs develop without it by keeping them at high

temperature fail, at least in the case of certain species (Carothers). This suggests the existence of a hereditary *rhythm of development* which does not depend, or depends only partly, on the external conditions.

It must not be forgotten, however, that the origin of the diapause may be connected with external conditions other than temperature. Thus, it seems that *moisture* is of considerable importance, as has been suggested by several observations. For instance, the embryonic diapause occurs in the development of at least some tropical species where it coincides with the dry season, and the larvæ hatch only after the first rains (Coleman, 1911 ; Coleman and Kuhni Kannan, 1911). In the experiments of Lounsbury (1910), the eggs of the Brown Locust preserved their vitality without developing (*i.e.* in a state of diapause) up to $3\frac{1}{2}$ years, if they did not get sufficient moisture, and the larvæ hatched even after that period as soon as the eggs were moistened. Unfortunately, no observations were made during these interesting experiments on the process of development of the embryo, and the stage that is able remain in a diapause for such a long period is still unknown.

The importance of moisture for the development of the eggs generally has been insisted on by many observers, but always somewhat vaguely. Some direct indications in this respect were obtained by Plotnikov (1911), who found that under laboratory conditions the development of the eggs of *Dociostaurus maroccanus* and *Calliptamus italicus* took place normally only when the eggs were well moistened. Water is, apparently, necessary for the development of the embryo, since it is absorbed by the eggs osmotically in considerable quantities, as has been found by Dampf (1925) for the eggs of *Schistocerca paranensis*, which in this way balance the loss of water through evaporation. It is not impossible, therefore, that the diapause in the eggs of the tropical species is caused directly by insufficient moisture during the corresponding months. The same cause may be partly responsible for the diapause in the eggs of the species of temperate regions where the second half of the summer is usually characterised by small amounts of rain.

The data relating to the effect on development of excessive moisture are exceedingly vague and do not permit of any safe conclusions. In the case of *Locusta migratoria* it is known that the places where its eggs are laid are often covered by the water of the spring floods for several weeks without any harmful effect on their vitality ; the hatching of the larvæ in such cases occurs in a normal way after the ground is dry, though the larvæ in flooded areas usually emerge later than those in neighbouring places that have not been flooded. This difference may be perhaps explained by the influence of temperature, not of moisture, since the eggs in the flooded ground are, of course, subjected to lower temperatures than those on the dry ground warmed by the sun.

The combined influence of heat and moisture on the development of grasshopper eggs has been studied by Parker (preliminary data published by Chapman, 1927). The eggs had been previously incubated under favourable environmental conditions (in moist sand) and placed in chambers with the moisture controlled by the use of sulphuric acid solutions and kept at

various constant temperatures. The percentage of the eggs which hatched under different moisture and temperature conditions is shown on a graph (Fig. 26).

Summarising all that has just been said about the influence of external factors on the development of the embryo in ACRIDIDÆ, we must admit that our knowledge on this point of great practical importance is very limited and very inexact. It is true that in addition to the facts discussed above there are in the literature many records of the dates of hatching of larvæ in different years and in different countries, but these are of no scientific value. What are really wanted are long series of carefully planned experiments on the development of embryo under different conditions. In such experiments it is clearly impossible to be content with the simple registration of the length

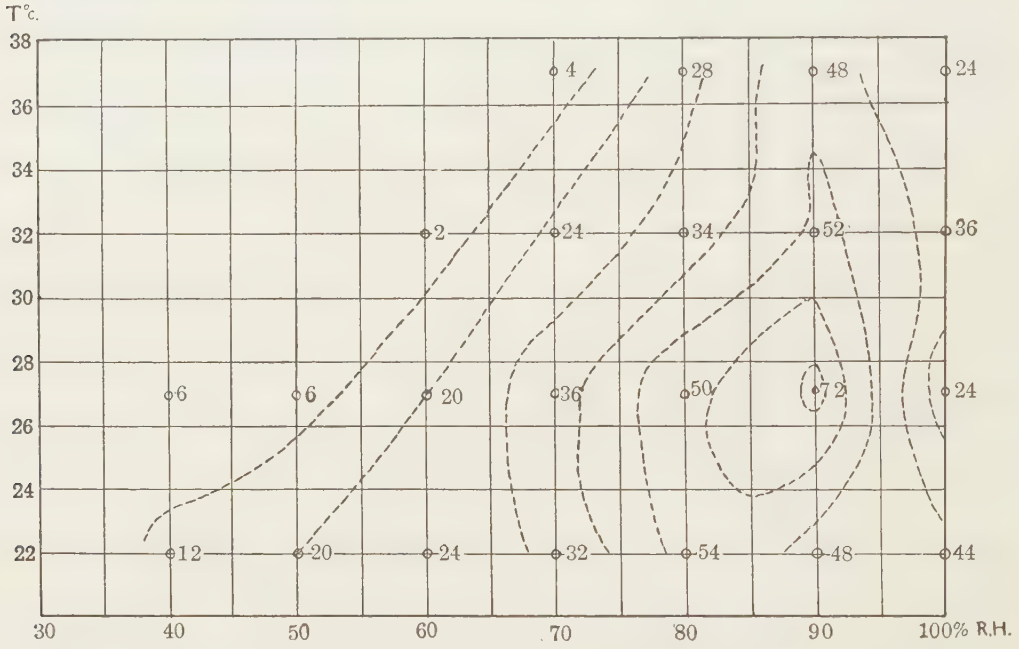

FIG. 26.—The percentage of eggs hatched under varying conditions of temperature and humidity ; dotted curves define the areas of equal effect (after Parker, in Chapman).

of the incubation period, and it is absolutely necessary to make exact observations on the actual progress of the development of the embryo ; then only may we hope to obtain some idea as to the factors influencing the rate of development in its different stages.

The study of the development of eggs under natural conditions is more difficult, since it is necessary to consider and to record exactly a whole series of factors. Thus the temperature of the ground in which the eggs are laid is influenced not only by the temperature of the air but also by the relative density of the vegetation, by the physical properties of the particular kind of soil, by the degree of exposure of the ground to direct sunlight, etc. Analogous conditions serve to complicate the study of the influence of moisture, while an exact estimation of the combined action of both factors is,

of course, still more complicated, though the difficulties in the way of such studies are not insurmountable. In any case the problem is one of outstanding practical importance and of great theoretical interest, and it is to be hoped that it will be attacked from various sides and by various methods.

Hatching of Larvæ

Changes in the Appearance of Eggs.—As has been already stated, the egg changes its outward appearance somewhat towards the time of hatching. It increases in size, but this is scarcely noticeable unless exact measurements are made ; it results, however, in the case of the species in which the egg-pod does not possess thick walls (*Locusta*, *Schistocerca*, *Calliptamus*), in the complete breaking up of the pods so that it becomes impossible to obtain complete ones. The colour of the eggs changes only in the very last days before hatching ; thus in the Moroccan locust the egg becomes greyish instead of yellowish, three days before hatching (La Baume, 1918). The degree of maturity of the egg is most easily estimated by the development of the eyes of the embryo, which are dark coloured and become visible even through the chorion about two weeks before hatching. The chorion itself becomes hyaline, and it is possible to see the larva through it, while the vitelline membrane loses its elasticity.

Conditions of Hatching.—The moment for hatching of the larvæ is determined not only by their maturity, but also by certain external conditions, *i.e.* the larvæ may be quite ready for hatching, but the process cannot begin without a stimulus. This is particularly well illustrated by the fact that often, when the eggs are quite mature, it is sufficient to dig them out of the ground for hatching to begin, while the eggs still in the ground do not do so. What the conditions are that stimulate the beginning of the hatching process, we do not know definitely. Unquestionably temperature is of considerable importance ; it must reach a certain point to stimulate the larvæ to activity, but exact observations in this direction are lacking, while the somewhat numerous records in the literature on the temperature of the air at the time of hatching have, obviously, only an indirect bearing on the subject and need not be discussed or collated.

The humidity of the soil must be a very important factor in hatching, since it appears that the rupture of the egg-shells is facilitated by a certain degree of humidity. This may be deduced from the commonly observed fact of a sudden mass hatching of larvæ after rain ; especially in the species of hot and dry countries, the rains are an absolutely necessary condition for the beginning of hatching. It may be suggested that the egg-shells, under the influence of moisture, become less elastic and easier for the larvæ to rupture.

Finally, light is also not without its influence on hatching. In the interesting experiments by Künckel, the eggs of the Moroccan locust kept in a dark box did not hatch as long as the box was closed, but hatching began immediately it was opened, only to stop again on its closing ; this could be repeated several times, but not indefinitely, and at last the hatching continued

even in the dark. More exact experiments on the influence of light have never been attempted.

The Mechanism of Hatching.—As stated above, the rupture of the egg-shells by the emerging larva is made easier by changes in their density. The latest observations by Dampf (1925) have shown that this must be connected with the fact that the larva, when ready to hatch, emits from its oral orifice drops of some fluid, which, according to that author, serves to soften the egg-shell. This must come from the stomach, and the phenomenon may be of the same order as the disgorging reflex of grasshoppers in their more advanced stages (see below, p. 67). The observations of Dampf are in agreement with the indication by Michelson (1922) that the oral orifice of the larva is open immediately on hatching, *i.e.* it pierces the first larval skin, and thus the larva can emit the fluid into the egg cavity. Michelson observed also that the larva just after hatching is already capable of emitting fluid from its mouth when irritated by touching its mandibles.

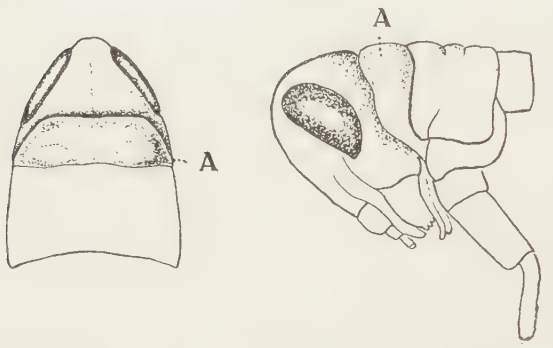

Fig. 27.—First larva of a grasshopper with the cervical ampulla (A) inflated (after Künckel).

The rupture of the egg-shell occurs as follows. The larva begins to move, at first feebly, then more and more energetically, twisting itself and wriggling. The thin membrane between the head and the pronotum begins to swell, forming two lateral inflations connected in the middle; these are the two parts of the *cervical ampulla* (Fig. 27, A). The ampulla pulsates, and this exercises a pressure on the egg cover, which usually ruptures opposite this point; the larva by strong wriggling movements of its body (not of its legs, which are enclosed by the first larval skin), gradually enlarges the opening and frees itself from the egg-shell. The latter is often torn into two parts, and the anterior one remains like a cap on the head of the larva until the emergence of the latter on the surface of the ground and even after the first moult.

The mechanism of the function of the cervical ampulla is not quite clear. It also plays an important part in the later stages of the larval life, particularly during the moults, when its functions are the same as at hatching. Künckel believed that the inflation of the ampulla is due to the larva swallowing air, which causes the alimentary canal to increase in volume and the blood to be forced into the cephalic portion of the body cavity. This explanation, while being apparently satisfactory with regard to subsequent moults, seems somewhat doubtful as applied to the process of hatching, since it is not clear that the amount of air (or other gas) inside the egg would be sufficient for the necessary inflation of the alimentary canal. Nikolsky (1925) pointed out that the inflation of the canal by air may be observed in a larva just hatched out

of the egg, but this observation does not throw a direct light on what is happening in the egg at the beginning of the hatching process.

The Vermiform Larva.—A larva which has just emerged from the egg does not look like the ordinary Acridid larva or hopper. Indeed, it scarcely differs in its general appearance from the fully developed embryo in the egg (Fig. 28). The head is somewhat bent downwards, its antennæ and legs lie close to the body, and the whole insect is enclosed in a transparent membrane, that envelops the whole body like a sack, but with separate "sleeves" for the antennæ, legs, and cerci (Michelson, 1922). All the older authors believed this membrane to be the *amnion*, *i.e.* one of the egg membranes, but the fact that it envelops each of the appendages separately is against this view. It is also chitinous and without cellular structure, as the amnion should be (Carothers, 1923). It is, thus, a true larval skin, and its shedding must be regarded as a regular moult and not as a continuation of the process of hatching.

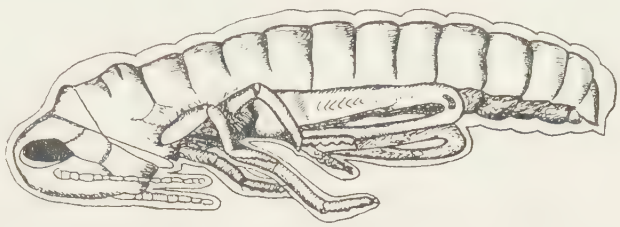

FIG. 28.—Vermiform larva of the Moroccan locust (after La Baume).

Emergence on the Surface.—Owing to the presence of the enveloping membrane, the emerging larva is unable to make efficient use of its appendages (Nikolsky, 1925), and moves, mainly, by means of the wriggling, worm-like movements of the abdomen. This mode of progression seems to be most suitable for the conditions, as the larva, after freeing itself from the egg, is still in the egg-pod and has to find its way to the surface. This capacity for vermiform movements together with the energetic action of the cervical ampulla (which alternately collapses and enables the larva to push its anterior portion into a narrow space and then inflates and forms a support for the hind portion of the body to be drawn up) is absolutely necessary for emergence. The larvæ of the species with thin-walled egg-pods make their way through the spongy stopper of the pod and through the thin layer of the soil above it; the larvæ of the species with hard egg-pods that are closed by a strong lid (Moroccan locust) must first of all lift the latter, as it cannot be penetrated (Fig. 29); how the larvæ succeed in doing this is not clear, but La Baume (1918) has suggested that the lid is lifted by the simultaneous pressure exerted by several larvæ reaching it together.

FIG. 29.—Emergence of vermiform larvæ of Moroccan locust from the egg-pod (after Künckel).

The greatest difficulties in emerging are necessarily experienced by the first larvæ that escape from a given egg-pod, since they have to form an exit.

Usually, though not always, all the larvæ from one egg-pod emerge practically simultaneously, and the first to do so are those from the upper eggs ; this is very interesting since the upper eggs are laid later than the others, and in the ovaries of the female they also mature later than the lower ones.

The causes that direct the movement of the emerging larvæ upwards have never been studied, although it is a phenomenon of considerable interest. Theoretically it may be suggested that phototropism of the larvæ plays a certain rôle, though, on the other hand, larvæ hatching in a glass jar containing earth move upwards along its transparent walls as usual. Apparently the movement is influenced by gravity (negative geotropism), and this suggestion is supported by the fact that the larvæ that emerge from an egg turned upside down also move upwards (Shapinsky, 1923).

Of practical interest would be an exact experimental study of the emergence of larvæ through layers of earth of various thickness and of varying physical properties, because this would give some indications of the possible effect of various agricultural methods on the emergence of the larvæ. In this direction, however, only some very crude experiments have been made by various authors, and the problem awaits serious investigation. From the data at hand, it may be only concluded that a mere increase in the thickness of the layer of the earth over the eggs can be scarcely of any influence ; in the experiments by Shapinsky (1923) larvæ emerged through a layer 24 inches thick.

Intermediate Moult.—Immediately on emerging on the surface, the larva, which is still worm-like in appearance, sheds its skin. The old authors believed the latter to be the amnion and considered this process to be the final stage of the process of hatching, while the vermiform larva was regarded as a special stage of the development of the embryo. As stated above, this view cannot now be retained, the hatching process being wholly completed within the egg-pod, while the vermiform larva is undoubtedly the *first larval stage*. La Baume (1918) quite correctly established the true character of the whole process, but, at the same time, he proposed to call the shedding of the first skin after the emergence, the *embryonic moult*, simply because the vermiform larva resembles the embryo in appearance more than the following larval stages. This name has been accepted by myself and by Nikolsky (1925), but now I consider it necessary to alter it, since it is incorrect in substance and therefore misleading. On the other hand, one cannot but agree with La Baume, that to call the vermiform larva simply the first larval stage, and the shedding of its skin the first moult, would be very inconvenient from the practical point of view, since it would involve an alteration in the total number of moults and stages. I believe, therefore, that it would be perfectly correct theoretically and convenient in practice, if we agree not to include the first larva in the general count of the stages and will call that larva—the vermiform larva, and the shedding of its skin—the intermediate moult.

This moult takes place practically simultaneously with the emergence of the larva on the surface, *i.e.* it begins during the later moments of the emergence and is completed immediately after it. The process of moulting itself is actually the same as that of hatching, and the cervical ampulla has

the same function. The whitish skins shed at the moult shrivel up into small whitish objects, and the surface of the ground becomes soon strewn with them (Plate I, Fig. 1).

Light is one of the factors that influence the intermediate moult ; larvæ hatched in darkness do not moult, but moulting begins immediately under the influence of light (La Baume, 1918). The mechanical effect of the surrounding earth is also of importance ; according to some observations (Michelson, 1922 ; Shapinsky, 1923), the intermediate moult sometimes takes place not on the surface, but when the larva reaches a cavity in the soil, in which case it is apparently stimulated by the cessation of pressure on it.

Thus the biological significance of the vermiform larva is that it enables the insect to emerge on the surface. Observations in the laboratory show that, if the intermediate moult has occurred for some reason before the larva has attained the surface, it dies without being able to emerge. In this connection it would be interesting to find out whether there is a vermiform larva and the length of its existence in such species as lay their eggs not in the soil, but in stems of plants and similar places, *e.g. Chrysochraon dispar.*

For the normal course of the intermediate moult certain conditions are necessary. Particularly important appears to be a definite degree of humidity of the air, on which depends the elasticity of the skin ; in moist air this becomes too elastic and difficult to burst so that the larva may die through being unable to shed it. Equally dangerous to the larva is an irregular moult, when the skin ruptures in the wrong place and it is unable to shed it in the usual way, a larva with a half-shed skin usually dying because it hampers its movements.

Development of Hoppers

Hopper of the First Stage.—After the intermediate moult, the larva loses its vermiform appearance and becomes similar to the adult insect (Fig. 30, A). The head of such a young hopper of the first stage attracts attention by its relatively very large size ; it is no longer bent downwards, and the front is vertical. The antennæ, legs, and mouth-parts become free and increase considerably in size compared with those of the vermiform larva ; the abdomen, on the contrary, appears shorter, and the total length of the body is less than in the latter.

The colour at first remains the same yellowish-white, but in a few minutes after the intermediate moult a distinct darkening of the colour begins ; at first, dark spots appear on various parts of the body, and gradually the whole hopper becomes dark, or even black, according to the species, and the pattern typical of the species makes its appearance.

This darkening is not due to the action of light, as might be expected, since the hoppers of *Locusta migratoria* become black even if they are kept in darkness (Michelson, 1922), nor does the blackening depend on the amount of light (Nikolsky, 1925). On the other hand, both these authors record that temperature influences the rapidity of the darkening process ; thus, at 7° C., there is no marked darkening even after three hours, while at 47° C. the hopper has already become black after 15 minutes.

There is little doubt that the process of development of the dark pigment is, as in other insects, that of oxidation, but so far no attempts whatever have been made to study the pigments of ACRIDIDÆ and their transformations, though the problem appears to be of outstanding importance, as we shall see later.

The Growth of the Hoppers.—The further development of the hoppers consists in the growth connected with the periodic moults. As has been stated above, the hopper after the intermediate moult has a very short and compressed abdomen, but it extends gradually, and after a few days the insect differs in appearance from what it was at the beginning of the first stage

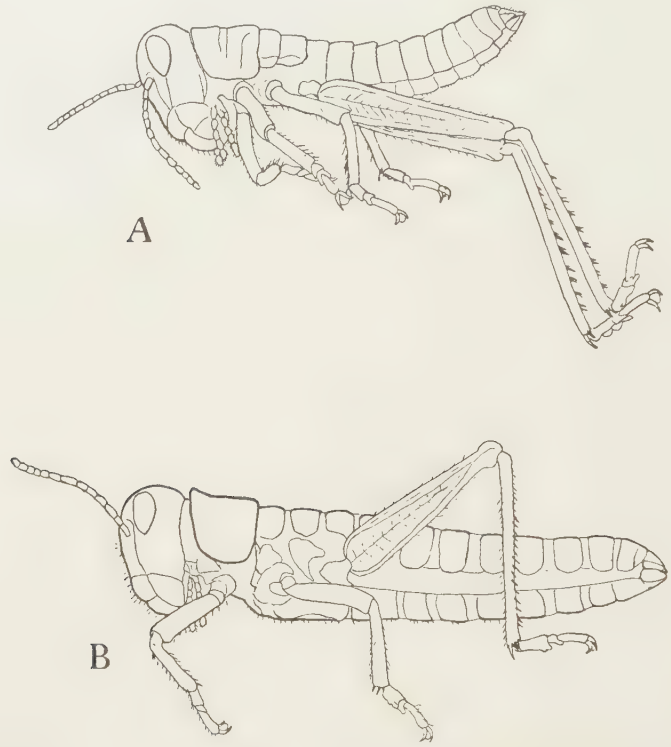

FIG. 30.—First stage larva of the Desert locust, A, at the beginning of the stage; B, at the end (after Vosseler).

(Fig. 30, B); its head, owing to the lengthening and thickening of the whole body, does not now appear to be abnormally large, although its absolute dimensions remain the same. This increase in the size of the whole insect is due, however, not to growth in the proper sense of the word, but merely to the expansion of the membranes connecting separate segments of the body, while the strongly chitinised parts of the latter (head, extremities) do not increase in size at all. This refers, however, mainly to the length of the appendages, since their thickness increases slightly towards the end of each stage, because the new chitinous envelope after each moult is a little larger than is immediately necessary; for instance, the muscles of the hind femur at first do not fill the whole space allotted to them, but develop gradually,

causing the femur to become more plump at the end of the stage than it was at the beginning (Vosseler, 1905).

Immediately after each moult, the total length of the hopper is the same as just before it, but it again appears macrocephalic, since the size of the head capsule has increased. Thus the growth of the whole hopper, as regards the length of its body, is more or less gradual, while the head and extremities increase in size by a series of jumps. Owing to this, it is possible to estimate the exact stage of the hoppers of a given species by measurements, for instance, of the hind femur. Lebedeva (1925) quotes the following figures for the length of the hind femur of *Locusta migratoria* in the different stages : I, 4 mm. ; II, 6 mm. ; III, 7–9 mm. ; IV, 12–14 mm. ; V, 17–20 mm. ; imago, 24–28 mm. This author thinks that the absolute length of the hind femur is the most reliable character for separating the stages, but she forgets that the absolute size of hoppers in this particular species may differ in various districts and in different years.

It is, therefore, more convenient, though not always absolutely reliable, to distinguish the stages by certain morphological changes during development, mainly in the structure of the antennæ, of the elytra and wings and of the end of abdomen.

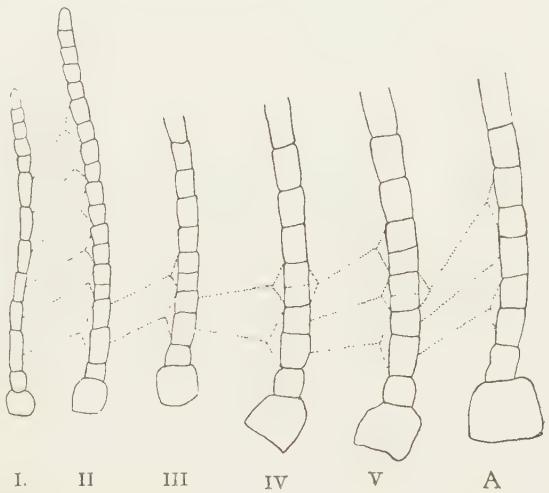

Fig. 31.—Postembryonic growth of the antennæ in the Migratory locust ; I–V, larval stages ; A, adult (after Takahashi).

The growth of the antennæ consists in the increase, after each moult, in the number of their joints owing to the division of single joints into two (Fig. 31). In the following table, the data on the number of the antennal joints in different species are collected together. The table was originally compiled by Takahashi (1925), but it is given here with some alterations and supplemented by data for *Dociostaurus maroccanus* (Sviridenko, 1925), *Locusta migratoria* (Lebedeva, 1925 ; Nikolsky, 1925), *Colemania sphenarioides* (Coleman, 1911), and *Hieroglyphus banian* (Coleman and Kuhni Kannan, 1911).

	Stages						
	I	II	III	IV	V	VI	VII
Locusta migratoria	13–14	15–19	20–21	22–23	24–25	—	—
Locusta migratorioides	13	19	21	22	24–25	—	—
Schistocerca americana	13	17	20–22	25	26	—	—
Melanoplus spretus	13	17	20–22	24–25	26	—	—
Melanoplus atlanis	12	15	17–18	21	23–24	—	—
Dociostaurus maroccanus	13	15–17	17–20	21–22	23–24	—	—
Colemania sphenarioides	8	9–10	10–12	13–15	15–17	17–18	—
Hieroglyphus banian	13	16–17	19–20	21–22	24–25	25–26	27–28

Numerous counts of the number of the antennal joints made by Lebedeva (1925) for *Locusta migratoria* have shown that some variations occur from the average figures, as given in the above table ; this makes the identification of the stages by this character alone liable to error ; these aberrations are, however, uncommon, and therefore of but little practical importance. Much more inconvenient in practice in the field is the necessity for using a strong magnification for making the counts, because the single joints are often very imperfectly separated.

Fairly reliable characters for separating the larval stages are presented by the *elytra* and *wings*. These develop only gradually as mere rudiments of the structures which may be observed in the adult insects. The theoretical course of their development is presented by Dovnar-Zapolsky (1926) as follows :

A. No rudiments perceptible ; hind margin of the mesonotum and of the metanotum rounded.

B. On the hind angles of the mesonotum and metanotum appear some rugosities ; in some cases a bow-shaped line separating the rudiments from the tergites is perceptible.

C. The rudiments assume the shape of well separated triangular lobes with a few raised longitudinal lines (rudimentary venation) ; the width of the elytral pads is about equal to the length of their hind margin.

D. The rudiments become longer, especially those of the first pair (elytra) ; the basal width of the latter becomes distinctly less than the length of the hind margin ; raised lines more numerous and distinct.

E. The rudiments, which in all the preceding stages were lying at the sides of the body, shift on to its back ; they turn round on their axis so that their outer surface becomes the inner ; and the rudiments of the first pair (elytra, attached to the mesonotum) cover the rudiments of the second pair (wings, attached to the metanotum) : the length of the second pair is shorter than the length of the pronotum along the median keel, and they do not extend beyond the first or second abdominal segment.

F. The rudiments retain the same position, but become longer ; the length of the second pair exceeds that of the pronotum, and they may reach to the third–fifth abdominal segment.

In the actual development of a given species all these stages may not be represented, and usually one or two phases drop out, while, on the other hand, two subsequent larval stages may retain practically the same phase of development of the rudiments. Phase A, which is known only in very few species (*Calliptamus italicus*), is the one that is most commonly absent, while the frequent description of the first larval stage in other species as absolutely without rudiments of elytra and wings has been proved in nearly all cases to be incorrect (Carothers, 1923 ; Nikolsky, 1925). In the majority of cases, the hopper after the intermediate moult appears with the rudiments in phase B, but sometimes even in D.

As an example of the course of the development of rudiments of elytra and wings, may serve a series of figures relating to *Locusta migratoria* (Fig. 32).

The hoppers in the last stages may be mistaken by an inexperienced

observer for the adult insects, possessing as they do abbreviated elytra and wings. The difference, however, is in the relative position of the organs: in the adults, the elytra always cover the wings; in the hoppers, the wing rudiments cover the elytral pads; in the hoppers only longitudinal veins are perceptible, while in the adults there are at least traces of transverse veinlets (Fig. 33).

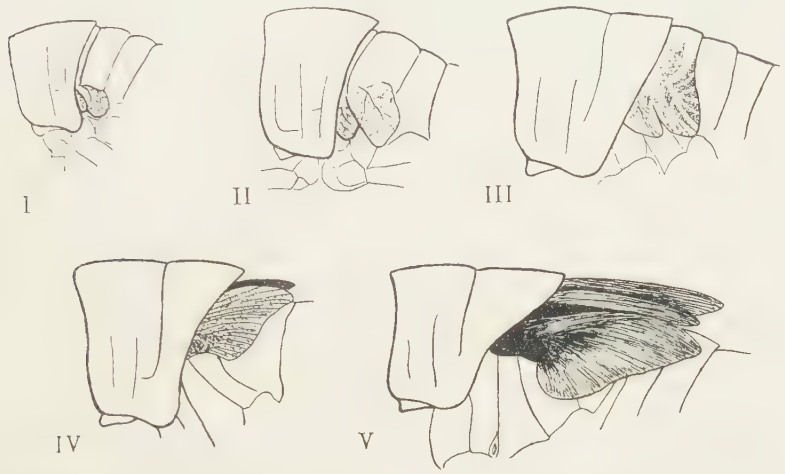

FIG. 32.—Postembryonic growth of the elytra and wings in the Migratory locust; I–V, larval stages (after Chang).

A gradual development also takes place in the terminal abdominal structures (Dovnar-Zapolsky, 1926). The cerci are already distinct in the first larval stage, when they are very short, and they grow at each moult. The difference between the two sexes is noticeable from the first stage. In the female (Fig. 34) there are on the underside of the abdomen two pairs of plates, which later will develop into the valves of the ovipositor. They

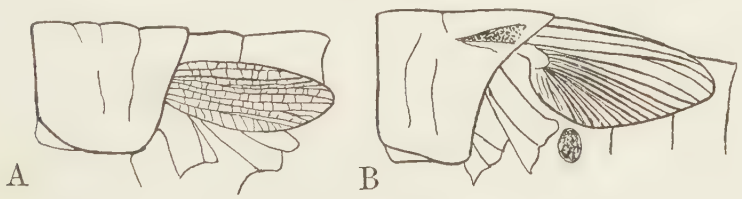

FIG. 33.—A, elytra of a brachypterous adult grasshopper; B, wing rudiments (covering those of the elytra) of a hopper of last stage (after Chopard).

increase in size after each moult; this is especially noticeable in the case of the anterior pair, which also gradually shift backwards and finally develop into the lower valves of the ovipositor. In a male of the first larval stage (Fig. 35) only one unpaired plate (sometimes forked at the hind end) is visible; in the following stages, the plate grows and forms finally the subgenital plate. (For detailed studies in the development of the terminal abdominal structures,

see also Coleman, 1911; Coleman and Kuhni Kannan, 1911; Nikolsky, 1925; Takahashi, 1925; Sokolow, 1926; Plotnikov, 1911.)

The development of the other morphological features of hoppers takes

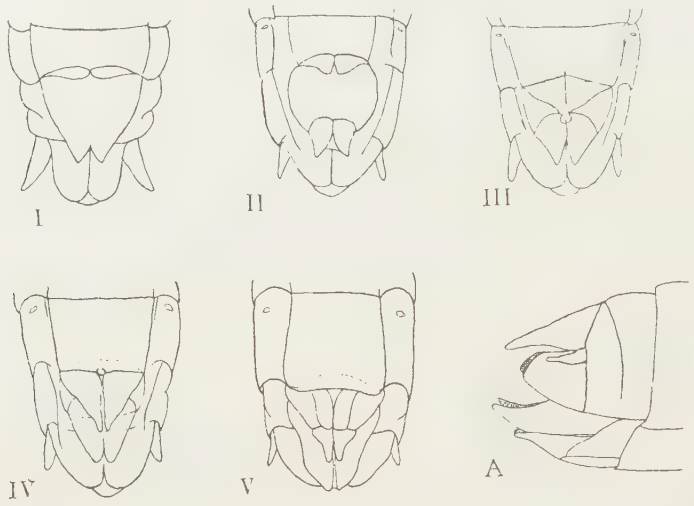

Fig. 34.—Postembryonic development of terminal abdominal structures in the female Migratory locust; I–V, larval stages, A, adult (after Takahashi).

place in such a manner that it is impossible to use them for practical purposes in distinguishing the stages. At the same time, many of the taxonomic characters used for separating the species or genera from each other appear at very early stages, so that it is possible to draw up keys for the determination of very young larvæ, as has been very successfully attempted by Dovnar-Zapolsky (1926) for the more common Russian species (see also Carothers, 1923). Even the fully developed embryo already exhibits certain characters typical of the adult of the species; thus, the number of spines on the hind tibiæ is the same in the embryo as in the adult (Carothers, *l.c.*).

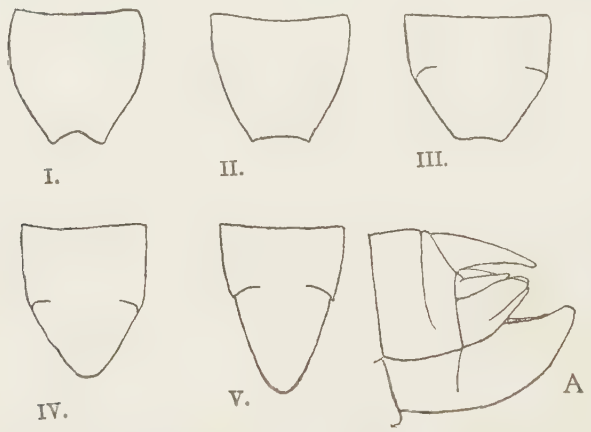

Fig. 35.—Postembryonic development of the terminal abdominal structure in the male Migratory locust; I–V, larval stages; A, adult (after Takahashi).

Moults.—The moults separating one larval stage from another are in substance only repetitions of the process of hatching or of the intermediate moult. During each moult, the cervical ampulla resumes its activity, and the function of the swallowed air becomes easily observable. The only

substantial difference between these moults and the intermediate one consists in the fact that the hopper, when preparing to moult, climbs a plant and hangs head downwards, utilising in this way the force of gravity for getting out of its old skin, which bursts on the back and remains hanging by the hind legs on the plant (Plate II). An exception to this rule is presented by the TETRIGIDÆ in which all moults occur on the ground, the hopper holding by its hind legs and gradually dragging itself out of the old skin (Hancock, 1902).

Coloration of Hoppers.—After each moult, the hopper is whitish in colour, and the darkening occurs gradually, as happens after the intermediate moult. In many species, the hoppers present the same details of the pattern as the adults; thus, the white X on the pronotum of *Dociostaurus maroccanus* is already apparent in the early stages; the pattern and the colour of the hind legs are also often as typical in the hoppers as in the adults. In the gregarious species (*i.e.* true locusts), another phenomenon is observed: their hoppers possess a special type of colour and pattern, highly typical for each species and even for each of the larval stages, but very different from those of the adults. A very remarkable feature of the coloration of the hoppers of all locusts is its uniformity in different and unrelated species living in different countries. The main features of this *swarming coloration* are the black and reddish or yellow colours, the black predominating in the earlier stages and gradually giving way to the others (Plate IX, Figs. 1–5). This phenomenon is the more interesting because the black colour in the hoppers of the solitary species occurs relatively seldom. The possible physiological rôle of the swarming coloration will be discussed later in connection with the behaviour of locusts.

The Number of Larval Stages.—Most of the species of ACRIDIDÆ that have been studied pass through five larval stages (always excepting the vermiform stage), but this is not a universal rule. Thus Bei-Bienko (1928) observed four larval stages in several species of grasshoppers in Siberia; the small brachypterous *Pezotettix giornae* has six larval stages (Dovnar-Zapolsky, 1926); in *Dociostaurus kraussi* the males pass through four stages, and the females through five (Plotnikov, 1926); in *Hieroglyphus banian* the males reach the adult stage after six moults, while the females pass through seven stages (Coleman, 1911); in *Colemania sphenarioides* there may be either five or six stages irrespective of the sex (Coleman and Kuhni Kannan, 1911). Nikolsky (1925), while stating that in *Locusta migratoria* there are always five stages, records an exceptional observation on a female individual which exhibited an additional, sixth, larval stage. This phenomenon has been studied in detail in the Rice Grasshopper (*Hieroglyphus banian*) by Coleman, who found that the separation of the hoppers into two groups occurs in the fourth stage, in which two degrees of development of the wing-pads may be observed. In some individuals the pads are more developed, and these pass through six stages, while in the others the pads are smaller, and an additional stage is required to bring their development in the adult to the same degree. When an additional stage is peculiar to the female only, this sex is usually considerably larger in the adult stage than the male; in *Colemania*, which

passes either through five or six stages, the size of the adults is very variable. The actual factors determining the number of moults in ACRIDIDÆ have never been studied.

THE ADULT AND ITS DEVELOPMENT

The final moult (Plate II), after which the adult insect appears, does not exhibit any substantial differences from the preceding moults, though outwardly this transformation seems more striking owing to the development of the organs of flight. Just after the larval skin is shed, the elytra and wings look like crumpled bits of rag hanging down the back ; the elytra now cover the wings, instead of being covered by them, as was the case in the last larval stage. The blood is then pumped into them ; in this process the swallowed air again plays a part, and they attain the normal size, harden, and can be folded in the usual way. The whole process of hardening and of attaining the normal coloration by all the chitinous parts occupies some hours, more or less, according to the external conditions.

Sexual Maturation.—By acquiring the organs of flight, the insect does not reach the final stage of its individual development, since it is not yet ready to pair, and a certain amount of time is required for sexual maturation. This process actually begins in the very early larval stages, and the rudiments of the ovaries and testes may be found even in larvæ of the first stage (Plotnikov, 1911) in the shape of an elongated plate lying in the hind third of the abdomen just under the dorsal blood vessel. If the plate is cleared of the connective tissue that closely surrounds it, it will be found that the rudiments in the case of a female are paired and that each consists of a series of small tubes ; rudiments of the testes consist of small round bodies, closely connected with each other ; in both cases a pair of rudimentary ducts issuing from the hind end may be also observed.

The above description by Plotnikov refers to *Dociostaurus maroccanus*, in which species a very early development of sexual organs is to be expected, since pairing in this species begins on the sixth day after the final moult (Sviridenko, 1924), and the genital products must be practically mature in the adults just after the moult. In this respect, however, very considerable difference may be observed in various species, and some of them require a very long period for the maturation of the genital products. Thus in *Patanga succincta* ten months pass between the final moult and pairing, and dissections of recently emerged adults show that their sexual organs are very small and little developed ; a marked increase in their size only begins after six months of the adult life (Lefroy, 1906). In this case there is a long period during which development of the genital products seems to stop ; such period of interruption in the development of the adult has been called the *imaginal diapause* by Pospelov (1911, 1922). This diapause is common to many ACRIDIDÆ, but is most clearly defined in the species that lead a gregarious life and migrate, *i.e.* the true locusts. This connection between the development of the genital products and the mass migrations of locusts communicates a special practical importance to the problem and should induce future investi-

gators to pay special attention to the study of the factors that regulate the development of the genitalia.

So far, very little experimental work has been done on these lines, but some suggestive results have already been obtained. Thus in the experiments of Pospelov (1926) with *Locusta migratoria*, the hoppers bred at a constant temperature of 35–38° C. and with the humidity at saturation point reached the adult stage and the adults soon started to pair and oviposit. On the contrary, the hoppers bred at 30° during the day and 20° at night, with the humidity at about 20 per cent., developed very slowly ; many of them did not reach the adult stage, while those that did so died without pairing. A study of the development of the genitalia showed that in both cases the ovaries of the recently moulted adults were very little developed, being only about 8 mm. long with scarcely perceptible egg-chambers in the tubes (Plate III, Fig. 1). In the females kept at 20–30° no further development of the ovaries took place, while in those kept at the higher temperature a considerable increase in the size and degree of development of the ovary was noticed after a month (Fig. 14). Field observations have also shown that in the newly emerged adults the degree of development of the ovaries was the same as in the experiments, and that in individuals after a migration they were as well developed as in the females kept at a high temperature.

In Pospelov's opinion, which it would be difficult not to accept, the migration flight carried out by individuals with immature genitalia results in an acceleration of their development owing to a rise in the body temperature during the flight. This must be due to the increased ventilation and more energetic oxidation of the fat-body and other stored products, which are especially consumed in connection with the last stages of sexual development ; in its earlier stages food is necessary for normal development, as stated by Plotnikov (1926).

Pospelov ascribes special importance in sexual maturation to the activities of the micro-organisms living symbiotically in the cells of the fat-body and in the blood ; to such organisms belong the *Coccobacillus acridiorum* of d'Herelle and certain Saccharomycetes. These organisms, according to Pospelov's theory, assimilate the stored products of the fat-body and then, in their turn, serve as food for the development of the genital products. His observations on the hoppers showed that the numbers of the coccobacilli increase at low temperatures (when they may become dangerous parasites instead of innocuous symbionts) and decrease at the higher temperatures. Thus the migration flight resulting in the increase of the body temperature may be a factor facilitating the process of assimilation of the symbionts and the maturation of the sexual products at their expense.

These observations and suggestions, of course, only prepare the ground for further and more detailed investigations, which are urgently wanted, since on them depends the elucidation of the important problem of locust migrations.

Chromosomes.—I will not dwell on the histological processes by which the germ cells transform into the genital cells, male—spermatozoa, and female

—eggs ; there is no substantial difference in these processes in the ACRIDIDÆ from those that can be observed in other animals. It is, however, worth saying a few words on the chromosomes of the genital cells.

A long series of papers on the North American ACRIDIDÆ, by McClung, several of his pupils and others, as well as by some European authors, have shown that the number of chromosomes in these insects is nearly always 23 in the somatic cells of the males and 24 in the females ; accordingly, at the division of the genital cells the number of chromosomes in each cell is 12 in the female, and 11 or 12 in the male. An exception is presented by the TETRIGIDÆ in which the number of chromosomes in the somatic cells is 13, and in the genital 7 and 6, respectively. This fact emphasises the fundamental difference of this group from other grasshoppers.

The shape and arrangement of the chromosomes is typical for various systematic groups of the ACRIDIDÆ. Thus, the genus *Mecostethus* may be recognised by the long stick-shaped chromosomes (in the first spermatocyte), while in other genera their shape may be variable (Fig. 36, A). Still more

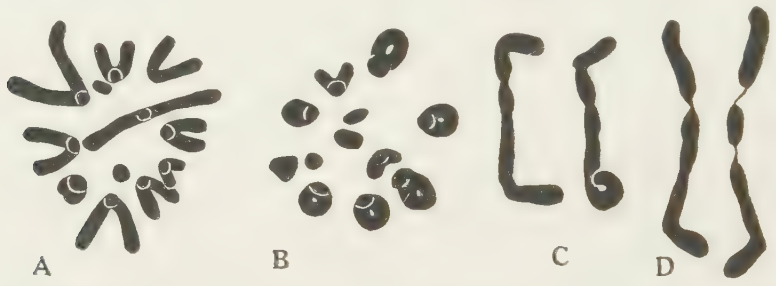

FIG. 36.—Chromosomes of A, *Mecostethus ;* B, *Tropidolophus ;* C, *Mermiria bivittata bivittata ;* D, *M. bivittata mcclungi* (after McClung).

interesting is the fact that in *Mermiria bivittata* McClung found it possible to separate two groups of individuals by the shape of chromosomes (Fig. 36, C, D) ; a detailed study of the external morphology of these groups convinced Rehn that they represent two different sub-species, which have been thus separated for the first time on the shape of their chromosomes.

Apart from their shape, the relative size of the individual chromosomes, their behaviour during the maturation process, and other details have been the subject of numerous works by various authors, who have found the ACRIDIDÆ a very convenient object for genetic studies, but we cannot enter here into these problems ; those interested in them must refer to the works of McClung, Carothers, Sutton, Robertson, Wenrich, Eisentraut, and an excellent summary given by Depdolla.

The Rate of Sexual Development in the Two Sexes.—The development of the genital products, at least in some cases, goes on at a different rate in the two sexes. Thus in *Anacridium aegyptium*, which reaches the adult stage in the autumn and then hibernates, the male genital products are already fully mature in October, while the ovaries remain very little developed until April.

In other species the development in both sexes is more or less parallel, but the spermatozoa usually mature before the eggs (Grassé, 1922).

Spermatozoa and Spermatophores.—The fully developed spermatozoa of the ACRIDIDÆ are somewhat variable in their general shape, though they have been little studied ; there are, however, no special features distinguishing them from those of other insects. They are usually collected in groups, called *spermatodesmae* (Fig. 37), but become separated in the receptaculum seminis (Boldyrev, 1927).

FIG. 37.—Spermatodesmæ of *Anacridium aegyptium* (original by Prof. Boldyrev).

Recent investigations by Boldyrev (1927), Iwanowa (1925), Sokolow (1925), and Fedorov (1927) have shown that the sperm is not directly transferred during copulation, but special tube-like structures, known as *spermatophores*, are formed. The spermatophore varies in size (only 2·2 mm. in *Calliptamus italicus* and up to 27 mm. in *Locusta migratoria*) ; during the pairing the hind end of the spermatophore remains in the canal of the penis, while the other end is in the female receptaculum seminis (Boldyrev, *l.c.*).

The spermatophores are formed at the beginning of the ejaculatory tract, but they here have no definite shape and are soft ; they harden and assume their proper shape in the terminal portion of the penis (Fedorov, 1927). The process of transferring the spermatophore and its further fate will be described later, when pairing is discussed.

Colour Changes of the Adults.—The extensive physiological changes that

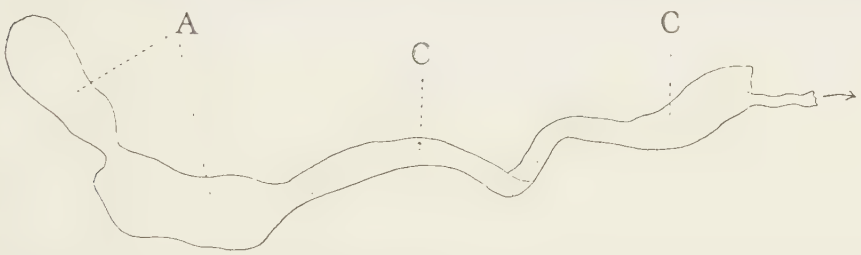

FIG. 38.—Spermatophore of *Anacridium aegyptium*.—A, ampulla with thin walls, containing the sperm.—C, canal through which the sperm comes out (original by Prof. Boldyrev).

occur during the development of the genital products find their external expression in changes of coloration. In the Desert locust, *Schistocerca gregaria*, this phenomenon was made known long ago by Künckel. In this species the adults for about a month after reaching that stage are of a wine-rose colour, which gradually changes to a brownish-yellow ; the intensity of the latter increases and fully mature individuals are of a brilliant yellow, the males being particularly brightly coloured, while the females are somewhat darker and have a greyish tint.

In the Indian *Patanga succincta* the colour changes are also very striking : the young adults have the general colour of the dry grass ; during the maturation of the genital products, a distinct purple hue appears, while

at the time of pairing and oviposition the dominating tint is brownish (Lefroy, 1906).

Less well marked, but still quite distinct, changes of coloration in connection with sexual maturity have been described by me in the European *Locusta migratoria ;* in this species the males acquire a bright yellow colour during pairing, while the females become dull-brown at the time of oviposition.

La Baume (1918) describes the process of colour changes in *Dociostaurus maroccanus* as follows : at first the colour of the hind tibiæ becomes more intensive ; then the occiput and the pronotum become lighter than before and the whitish X-shaped design on the pronotum becomes consequently less sharp ; finally, a distinct yellowish tint appears, particularly on the front ; generally speaking, mature individuals differ from young ones by the paler general coloration and less sharply defined pattern.

On the whole, in a number of species it is possible to estimate the degree of the maturity by the coloration, and this has a great practical importance, enabling one to conclude from the external appearance of the individuals in a given swarm whether there is an immediate danger of oviposition or not.

The physiological side of the changes in coloration has been very little studied. Vosseler (1905) thought that the appearance of the yellow tint in the African locust must be connected with the dissolution of the fat-body, the yellow pigment being a by-product that remains after the reserve material from the fat-body is used for building up the genital products ; these suggestions, though illustrated by microscopical examination of the fat-body, were not based on detailed studies. According to La Baume (1918), there is no direct physiological connection between the colour changes and the development of the genital products, since they occur approximately at the same time in both sexes, while maturation in the female is more retarded than in the male ; this author believes that the changes in the colour are due to the processes of senility, which, however, does not explain this interesting phenomenon, and it is to be hoped that detailed physiological studies on it will be undertaken by someone.

Pairing and Oviposition

Pairing.—The proportion of the sexes at the time of pairing is recorded in the literature in respect of very few species only ; in *Dociostaurus maroccanus* the males predominate, from 55–76 per cent. of the total number of individuals belonging to that sex (La Baume, 1918 ; Sviridenko, 1924).

The process of courting the female is very simple and short, consisting mainly in stridulation, which must be regarded as an expression of sexual excitation. The suggestion that stridulation serves for the attraction of the females by the males is not based on actual observations, while it seems doubtful whether the females can hear it at all. Apart from stridulation, the males sometimes stroke the female with their antennæ. In the flightless *Podisma pedestris,* which cannot stridulate, the whole behaviour of the male is very peculiar. Whereas in the stridulating species the male tries to find a female, instead of waiting until it is "attracted," and approaches it openly, in

Podisma the male lies in ambush until a female approaches and then jumps on it suddenly, without the preliminary stroking with the antennæ (Poulton, 1896). The same habits have been observed, however, in other, winged, species also (Fedorov, 1927, in *Anacridium aegyptium*).

Pairing does not always indicate sexual maturity : in *Anacridium aegyptium* the female often pairs when the eggs in her ovaries are far from being mature, so that development of the genital products and of the sexual instinct are disconnected (Grassé, 1922).

Abnormal pairing by individuals of two different species has been observed repeatedly ; thus, La Baume records cases between the males of *Dociostaurus maroccanus* and the females of *Calliptamus italicus* or of *Oedaleus decorus*. Still commoner are cases of males pairing with the dead bodies of females. While it may be safely supposed that no actual copulation takes place in such cases, these facts seem to indicate that the males find the opposite sex mainly by means of their very imperfect sight.

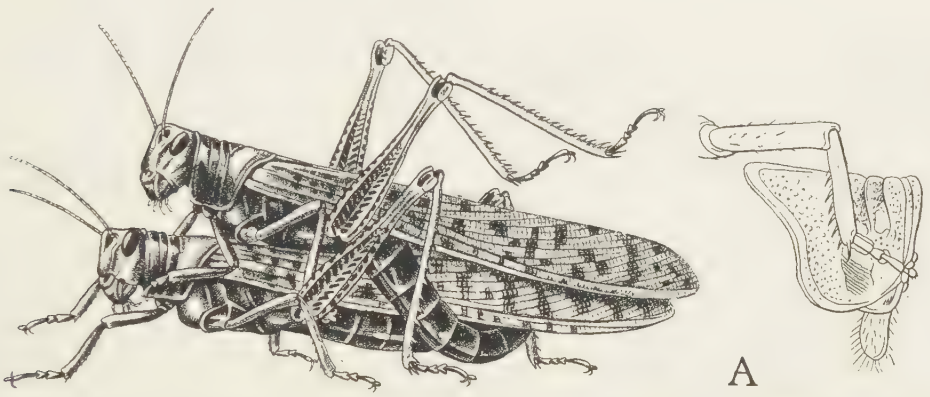

Fig. 39.—Copulating pair of the Desert locust.—A, front leg of the male clasping female pronotum (after Künckel).

During pairing the male sits on the female (Fig. 39) so that his front is just above her occiput and his front legs clasp the pronotum of the female, their claws interlacing at its lower margin (A) ; the middle legs are attached by their claws to the mesothorax of the female near the base of her middle legs, while the hind legs of the male remain unemployed, and pairing can take place even if they are removed (Grassé, 1922).

Having established himself firmly, the male lowers and then twists his abdomen sideways ; the cerci are raised, the subgenital plate bent far backwards and the penis, protruding from its membranous hoods, feels its way between the lower valves of the female ovipositor. Then the male cerci clasp the female subgenital plate and the penis enters the opening of the receptaculum seminis (Fedorov, 1927).

A pair sometimes remains in copula for several hours, in some species occasionally as long as two days. They are not easily frightened ; the female can walk and even make little jumps, but cannot of course fly. The male from time to time makes movements with its hind legs as if for stridulation,

and this has been observed even in the species that cannot produce sounds, thus corroborating the idea that these movements, whether the sound is produced or not, are merely an expression of sexual excitement.

The duration of the period of copulation is, apparently, intimately connected with the process of formation of the spermatophores, in which the sperm is transferred into the receptaculum seminis of the female. In many species only one spermatophore is formed and transferred, and pairing is accordingly shorter than in others, where the spermatophores are numerous and are transferred one after another as they are formed, as happens in *Anacridium aegyptium* (Fedorov, 1927). In this species Fedorov found from 6 to 30 spermatophores formed during a single pairing lasting from 18 to 60 hours.

The spermatophores in the receptaculum seminis of the female are emptied of sperm and then ejected from the receptaculum accompanied by a certain amount of sperm, which, in the case of numerous spermatophores, glues them together. They form a mass between the lower valves of the ovipositor, and such masses of empty spermatophores at first resemble jelly; they then harden and become brittle, and the female loses them bit by bit. Soon only a few flakes remain; by their presence, however, it is possible to recognise a fertilised female long after pairing has occurred (up to a fortnight in *Acrida turrita;* Boldyrev, 1927).

As the number of females is often far less than that of the males, several of the latter may be observed attacking one female, and something like fights for the possession of a female are not infrequent.

The number of pairings that take place before the first batch of the eggs is laid has not been established by observations. In any case oviposition does not immediately follow pairing, and it must be presumed that the sperm in the receptaculum seminis may be preserved for a considerable period and used when necessary. Both males and females are known to pair repeatedly.

Parthenogenesis.—Fertilisation in the ACRIDIDÆ does not constitute an absolute condition for the development of eggs, since numerous cases of parthenogenesis are known. This phenomenon has been observed in *Locusta migratoria*, *Dociostaurus maroccanus*, *Calliptamus italicus* (Plotnikov, 1915), and *Locustana pardalina* (Faure, 1923), but in none of these cases was it proved that the progeny could reach the adult stage or reproduce themselves. Very definite data are available only with regard to one American Tetrigid, *Apotettix eurycephalus*, which Nabours (1925) bred in large quantities for his studies in heredity. Of a total number of nearly 200,000 individuals used in his experiments not less than 5000 were obtained parthenogenetically. Normally parthenogenetic eggs produce females, and these are able in their turn to produce a progeny either parthenogenetically or when fertilised; in one case seven consecutive parthenogenetic generations were obtained. Out of the whole number of 5000 individuals only 13 were males, and only one of these proved to be able to fertilise a female. The productivity of the parthenogenetic females proved to be far below the normal, the average number of eggs laid being about one-third of that laid by fertilised females. In some experiments it was observed that one female may lay both fertilised

and parthenogenetic eggs. All these observations indicate, at least, that parthenogenesis in ACRIDIDÆ can occasionally play a part in the preservation of the species.

Oviposition.—The great majority of the ACRIDIDÆ lay their eggs in the ground, and the general character of the places selected for this is more or less constant for each species, as will be more fully discussed in the chapter on ecology. The female spends some time in choosing a place for depositing each batch of eggs. What the requirements to be satisfied for this are, we do not yet know, but the greatest importance seems to be attached to the physical properties of the soil and, perhaps, to its humidity. With regard to the hardness of the soil, a considerable difference may be observed between the different species; thus, the Moroccan locust (*Dociostaurus maroccanus*) lays its eggs preferably in hard uncultivated soils, while *Locusta migratoria* selects soft soils, including those actually under cultivation. A study of the preferences of each species for definite kinds of soils might be apparently easily made under laboratory conditions in special cages, each containing several different samples of soil, but nothing has yet been done in this direction.

Descriptions of the actual process of oviposition have been given by many authors, but the best so far seems to be that of Fedorov (1927), who deals with *Anacridium aegyptium*, and the following is largely based on his paper.

Females ready for oviposition become markedly restless; they crawl to and fro, and their ovipositor begins to make movements as if digging; sometimes, even digging itself begins, only to be interrupted, apparently because of unsuitable soil. Owing to these abortive attempts at digging, the surface of the soil at places where a swarm of locusts is ovipositing usually bears numerous pits and shallow burrows. When beginning to dig a regular burrow, the female rises high on the two first pairs of legs, slightly supporting itself also by the hind pair, while the abdomen is strongly arched with its end perpendicular to the surface of the soil; according to Grassé (1922), the hind pair of legs does not actually take part in the process, and digging and oviposition occur normally in females in which the hind legs are lacking. In the digging itself, the main work is done by the valves of the ovipositor, which make two kinds of movements. At first, they are all collected together, forming a wedge-like tool that enters the soil under pressure of the abdomen; then, the upper and lower valves open and the hole is thus widened; they then close and are pressed again, then again opened, and so on; in this way a burrow is made, and the ovipositor enters deeper and deeper into the soil, while the abdomen elongates. This elongation of the abdomen is due to the expansion of the membranes between the 4th to 8th abdominal segments (Fig. 40). The extension of the abdomen may be almost incredible; in *Anacridium aegyptium* the normal length of the abdomen is about $3\frac{1}{2}$ cm., but it may become elongated up to 9 or 10 cm. To give the burrow a circular shape, the female from time to time contracts the abdomen and corrects the work already done by twisting the end of it through 90°, now to the right, now to the left.

It is obvious that the expansion of the abdomen, together with the move-

ments of the valves, is very important in digging the burrow, but the question arises as to the causes of this expansion. Künckel suggested that it is due mainly to the pumping of blood into the abdomen, in a way similar to that described in moulting. Grassé (1922), however, believes that the amount of blood in the body would be quite insufficient for this purpose, and the expansion, in his opinion, is caused by air swallowed into the stomach, and artificial pumping of air into the stomach has produced the same effects. Fedorov (*l.c.*) thinks that the expansion is due entirely to the air-sacs; according to his observations, when the abdomen is fully extended, one can see its rhythmical movements, which apparently facilitate the work of the

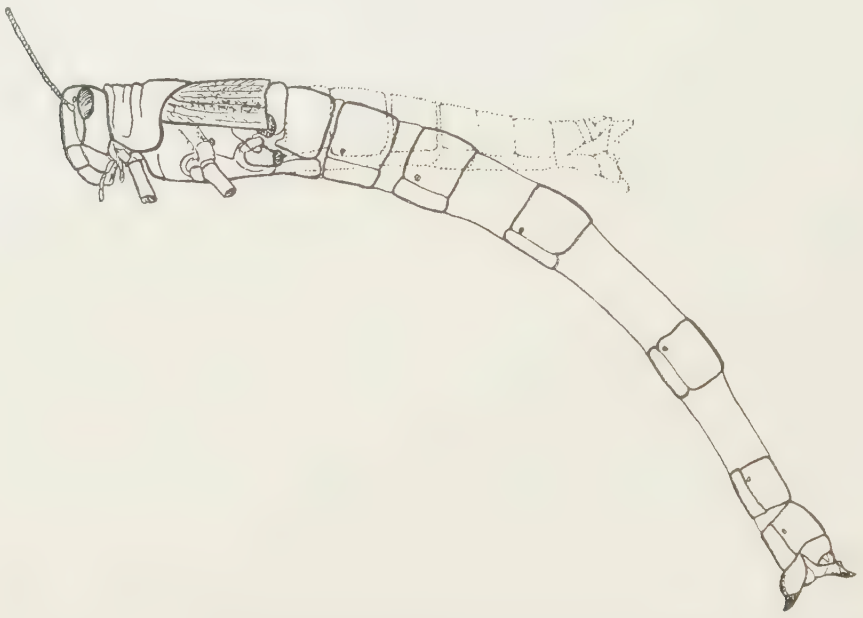

FIG. 40.—Extension of abdomen of female Desert Locust during oviposition; dotted outline shows the normal size of the abdomen (after Vosseler).

spiracles and result in the filling of the air-sacs with air; movements of the head and of the mouth-parts, which are observed during the act, he connects with this pumping of the air into the air-sacs, though it seems that these movements support Grassé's idea of pumping the air into the stomach; perhaps both these authors are right, and the air is pumped both into the air-sacs and into the stomach also. One point that is quite clear in any case is that the muscles of the abdomen play no part in the digging process, except for turning the abdomen as described, and for the movements of the valves.

The shape of the burrow depends to a great extent on the density of the soil. In soils that are not too loose, it is usually more or less curved backwards (Fig. 41), but in very soft soils the burrow may be perfectly straight and vertical (*Colemania sphenarioides;* Coleman, 1911). The curvature of the abdomen forwards, as often figured, does not and cannot happen, under any conditions.

When the burrow is ready, oviposition itself begins. First the abdomen is slightly contracted, and the female begins to emit the foamy material secreted by the accessory glands. The eggs, enveloped in a thin foamy film, appear one after another through the aperture in the closed valves and are laid with their micropylar ends downwards. The abdomen gradually contracts, and at the completion of the process, assumes its normal length. When all the eggs are laid, only the foamy material is emitted, and this serves to form the stopper, or lid, of the egg-pod.

The secretion of the accessory glands, which forms the foamy substance and later hardens into the walls of the egg-pod, has been studied with regard to its chemical properties by Giardina (1901) in *Pamphagus marmoratus*. According to this author, the secretion is a viscous fluid, an albuminoid of the keratine group, resembling in all its reactions the substance of which the oothecæ of cockroaches and Mantids are formed. Ito (1924), however, while confirming the proteid character of the secretion, points out that it is very different in its properties from that of which the oothecæ of cockroaches and Mantids consist, and he accounts for this by the different origin of the secretion, that of the Acridids being derived from mesodermal cells, while in the two other groups the secreting cells are ectodermal in their origin.

Fig. 41.—Female grasshopper ovipositing (redrawn, after Gibson).

In any case, the function of the secretion seems fairly clear: it must be protective, especially from excessive moisture, or drought; on the other hand, it partly glues the eggs together. The protective function in many cases is further strengthened by the secretion soaking into the adjacent layer of soil, which, after the secretion has hardened, forms a very strong and hard egg-pod.

The whole process of oviposition lasts about an hour. After it is completed, the female of many species covers the entrance to the burrow with particles of soil, trampling them down with the hind legs or with the ovipositor (*Podisma pedestris;* Shapinsky, 1923).

In some species (*Locusta*, *Dociostaurus*), the male during the whole process of oviposition sits on the female's back and pairs with it immediately it is completed. Oviposition can, however, take place in the absence of the male, and in certain species this is the rule (*Anacridium aegyptium;* Grassé; Fedorov).

It has not yet been established definitely whether both the ovaries of the female empty themselves of all their mature eggs at the same time, though Grassé observed that in *Anacridium aegyptium* only one or two eggs remained in them. Coleman (1911) observed that in *Hieroglyphus banian* one ovary empties after the other.

There are a few species of ACRIDIDÆ that do not lay their eggs in the ground, *e.g. Chrysochraon dispar*, which oviposits in the hollow stems of weeds, in cracks in the bark of trees, etc. (Shapinsky, 1923*a* ; Ramme, 1927). The smaller rice grasshopper of India (*Oxya*) lays its eggs in the ground, but when the rice-fields are under water, it lays in the clumps of rice, between the stems (Ramachandra Rao, 1921).

The *egg-pods*, which are the result of oviposition, present a considerable variety of structure, and this makes it possible to recognise the species to which a given egg-pod belongs. However, only in a relatively small number of species (mainly Russian) have the egg-pods been studied, and the subject offers a large field for study by any entomologist ; the practical importance

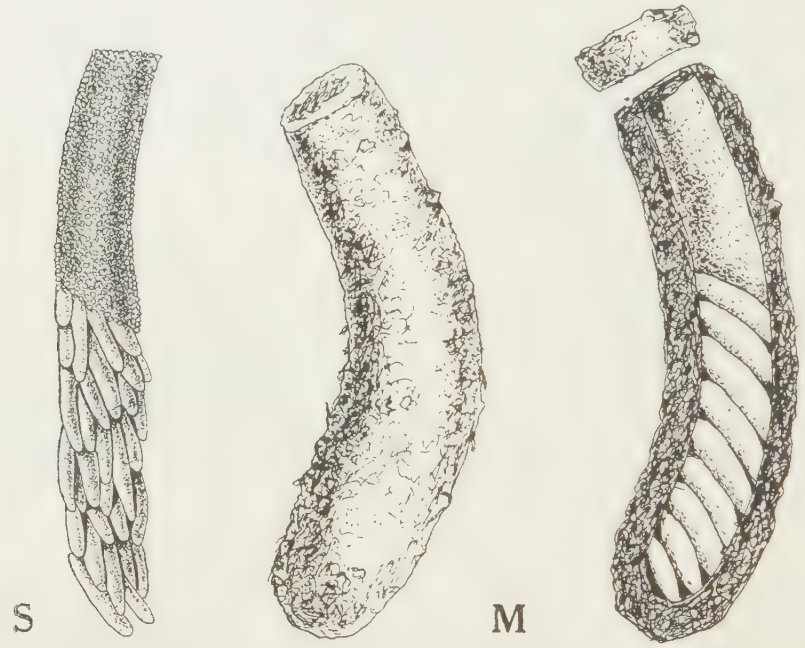

FIG. 42.—S, Egg-pods of Desert locust (natural size ; after Künckel), and M, of Moroccan locust (enlarged, outer view and open ; after La Baume).

of this work is obvious, while from the scientific point of view, such a mass of entirely new facts could be collected (especially by an observer in tropical countries). that even the mere recording of them should be of great value.

The egg-pods are formed mainly by the secretion of the accessory glands ; the quality and the quantity of the secretion apparently determines the structure of the egg-pod. The simplest type of pod may be observed in *Anacridium aegyptium* and particularly in species of *Schistocerca*, in which the eggs are scarcely glued together and there is no proper wall (Fig. 42, S).

A classification of egg-pods was recently suggested by Vorontsovsky (1924, 1926*a*). He distinguishes two types, those composed only of the secretion without any foreign admixture, and those the walls of which are largely composed of particles of soil glued together by the secretion.

In the first type there are four main different forms: bursa, capsule, pill, and flask, while in the second type the pods are of two kinds—those made of cemented earth, very hard and strong, and easily breakable earthen pods that are not cemented.

The interior of the pods is also very variable. There may be one chamber, or there may be a partition dividing the cavity into two. In the first case the eggs may fill the whole chamber, or there may be a space above them, either empty, or filled with the porous, spongy mass formed of the dried foamy secretion. In the double-chambered pods, the upper chamber is usually filled by the spongy mass, or in its lower portion there are several membranous partitions with empty spaces between them.

The outer opening of the pods is usually closed by variously formed devices, like a stopper entering the pod, or a disc-like flat lid (Fig. 42, M).

In rare cases the eggs in the pod lie quite freely, not glued together or to the walls, so that they may be shaken out of the pod (*Dociostaurus kraussi*). In most cases, however, the eggs are glued together by the secretion and placed in a definite order that is characteristic of the species, usually in two or four rows. The number of eggs in a pod varies even in the same species, though within definite limits; the smallest number may be observed in some species of *Stenobothrus*, which have pods with 2–10 eggs in each; while in large species, like *Locusta* or *Schistocerca*, there are often over 100 eggs in one pod.

The Number of Egg-Pods.—The problem of the number of egg-pods that may be deposited by a single female is of great practical importance. It may be considered as firmly established that the normal number is more than one. In captivity the females may live a very long time and lay their eggs at short intervals; thus in the South African Brown Locust (*Locustana pardalina*) up to fourteen egg-pods have been obtained from one female (Faure, 1922), and analogous figures are known for other species, but this cannot be regarded as anything approaching a proof that the same happens in nature. In the case of the Moroccan locust, Sviridenko (1924), on the ground of field observations, accepts two or three pods, but La Baume (1918) believes that only one is laid. The problem has not been studied at all in the case of the solitary species.

Towards the end of the oviposition period, a considerable excess in the number of females over that of the males is usually observed, since the males die off first. Death of the females concludes the life-cycle.

Annual Cycle

It is possible under laboratory conditions, at the optimum temperature and moisture, to observe in certain species of Acrididæ a continuous development, with several generations during a year (*Chortophaga*; Carothers, 1923). In nature, however, such conditions are hardly fulfilled in any climate, and there are no reliable records in the literature of even three full generations a year in any species; even two generations are definitely known only for very few of the species studied. It is possible, of course, that detailed observations

on the life-cycles of tropical species would reveal cases of continuous development in some cases, but it seems that even there one generation a year is the normal, as is the case with *Aularches miliaris* in Ceylon (Hutson, 1926), and in the vast majority of ACRIDIDÆ of temperate climates. The cause of this is the *diapauses*, or interruptions in the development which may happen at different periods of life and are partly a direct result of the influence of external conditions and partly depend on the inherited *developmental rhythm*.

The cycle that is most typical for the majority of ACRIDIDÆ seems to be the one in which the diapause occurs in the egg-stage, the eggs lying without development in the soil for several months, these coinciding in temperate climates with the winter and in the tropics with the dry season. It is important to note that the interruption in the development of the embryo in the egg does not always occur under the direct influence of a low temperature or excessive dryness ; in many species of temperate climates, as we know, the diapause begins when the temperature is far above the developmental zero (see p. 36). Artificial interruption of the diapause is possible only in certain cases, and these seem to fall into two categories. Firstly, it is possible in the species that are widely distributed and that in warmer climates normally produce more than one generation a year ; in this case the diapause under colder conditions must be due to the direct influence of external conditions, and changes in the latter may break the diapause. In the second group, the diapause may be forcibly broken in certain species that are able to produce two different phases or biological forms, one of which is inclined to continuous development under favourable conditions (see p. 36).

In other species attempts to break the diapause forcibly give no results, and this leads to the conclusion that they possess an inherited annual life-cycle, or developmental rhythm, corresponding to the average climatic conditions of a given country. The advantage derived from the rhythm is obvious ; if the eggs developed without a diapause, the cold winter weather in temperate regions or the droughts of tropical countries might have coincided with the larval stage, in which the insects are much more susceptible to unfavourable conditions than in the egg-stage. It must be frankly admitted, however, that our present knowledge on the subject of rhythm is very inadequate, and further laboratory investigations, supported by extensive field observations, especially in the tropics, are urgently wanted.

The second type of annual cycle is characterised by an imaginal diapause covering up to five-sixths of the whole period of life. As an example may serve *Patanga succincta*, in which ten months pass between the last moult and the oviposition. Here also belong some of the species of temperate regions, such as *Anacridium aegyptium*, *Acrotylus insubricus*, etc. ; these only reach the adult stage late in summer, or in the autumn, and only begin to oviposit in the next spring. There is some reason to suggest that this type of development corresponds to the conditions of existence in subtropical countries of the Northern hemisphere where a dry period corresponds to our winter. A study of the geographical distribution of such species and of their relatives show that all such species in the fauna of temperate regions are

either geologically recent migrants from the south, or may be regarded as relics of a subtropical fauna inhabiting the same countries at some former geological period with a warmer climate. In connection with this it is of great interest to quote some curious observations made by Nikolsky (1925) in Turkestan on *Acrotylus insubricus*. This species hibernates in the adult stage, and, when the temperature drops below 10° C., it buries itself in the soil ; in autumn it does this every night, coming out again in the morning, but later in the season it does not emerge at all until the spring.

It is very remarkable that in the species with this second type of annual cycle the rhythm of development is also very firmly established and cannot be altered forcibly. Thus, females of *Anacridium aegyptium* which had been kept throughout the winter at a temperature of 30° C. and well fed, when dissected in December, showed the same degree of development of the ovaries as the individuals hibernating in the field (Grassé, 1923).

In some species of this second group, the individuals do not all hibernate in the adult stage, but some of them pass the winter as larvæ. The same thing regularly happens in certain other species ; thus, *Pyrgomorpha conica*, Pamphaginæ, and some other species normally hibernate as hoppers.

Physiology of Hibernation.—Interesting physiological studies on hibernating grasshoppers were recently made by Bodine (1921, 1923). From the point of view of ability to withstand the winter cold, it is a fact of great importance that the water contents of the body of a hibernating grasshopper is far below that in summer, dropping from 72 to 65 per cent., and increasing again in spring. The output of CO_2 which serves to indicate the energy of metabolic processes is in hibernating grasshoppers 8–10 times lower than normal.

CHAPTER IV

BEHAVIOUR

Methods of Movement

The vermiform larva just after hatching from the egg reaches the surface of the soil by means of the peculiar movements described above (see p. 41). After the intermediate moult, the hopper is able to move in several different ways, the simplest of these being *crawling*. Exact observations on the mechanism of this crawling are lacking, but it may be stated that all three pairs of legs take part, though the hind pair does not seem to play a very active rôle. The velocity of movement by crawling has been estimated by Nikolsky (1925) for the hoppers of *Locusta migratoria* in the fifth stage at 23 feet a minute. This figure is, however, purely theoretical, as normally the hoppers of all gregarious species during mass migrations do not move all the time by crawling, but alternately crawl and jump. No one has ever studied the movements of the solitary species, but apparently they mostly crawl, while jumping appears with them to be only a reflex movement when stimulated ; the same seems to apply to the species that are flightless in the adult stage.

A slight modification of crawling is the *climbing* of plants. During this action the first two pairs of legs are moved first, then the hind pair ; when the latter is fixed at a new spot, the two others are moved again, etc. (Grassé, 1922). An important part in climbing must be taken by the pulvilli between the tarsal claws, which, as a rule, are better developed in the species that live mainly on plants (phytophiles, like *Podisma*, *Anacridium*, etc.), while they are very small, or even absent, in the geophilous species (Œdipodinæ, Tetrigidæ).

The best-known method of movement in Acrididæ is *jumping*, or hopping, from which the common names of the group are derived in many languages (grasshopper, sauterelle, saltamonta, skakalez). It is mainly by a series of jumps that the mass migrations of larval bands are made, while the jumps are also a result of various stimuli, as will be seen later.

Both the hoppers and the adults of certain species are able to *swim*. Amongst the Tetrigidæ there are a number of semi-aquatic species that live near water and swim quite voluntarily. Apart from these, there are species in other groups that live on water grasses and can swim perfectly well (*Euprepocnemis*, *Oxya*). In some of them special adaptations for swimming may be found, *e.g.* expansion of the margins of the tibiæ and of the first tarsal joints. The mechanism of swimming does not differ essentially from that of jumping, since the main rôle is taken by the hind legs, which make jerking movements,

while the two other pairs move only a little, or not at all. It is very interesting that a swimming insect has its body half submerged in the water and carries a supply of air under its pronotum so that it can enter the tracheal system through the first thoracic spiracle. To change the air, the insect turns on its side and, raising the hind margin of the pronotum, takes a bubble of fresh air under it (Takahashi, 1921). This explains how hoppers are able to swim for a long time ; in the experiments by Nikolsky (1925) hoppers of the third stage of *Locusta migratoria* could swim for 7 to 12 hours, and those of the fifth stage from 13 to 28 hours.

Flying is of course possible only in such species as possess fully developed wings in the adult stage. Taking off from the ground is actually a jump simultaneous with the spreading of the wings, but the jump is not absolutely necessary, since a grasshopper can take off from a plant, or with its hind legs cut off (Nikolsky, 1925). During flight, the wings and elytra beat independently and not even synchronously ; the front and middle legs are somewhat pressed to the thorax, as in the resting position, while the hind legs are more or less bent at the knee (Plate IV), and not stretched straight backwards, as they are usually figured. Flight sometimes has a passive character as when swarms drift with the wind, but flight against a moderate wind is not impossible. It is often suggested that the flight of locusts is greatly assisted by the air-sacs, which when filled reduce the specific gravity of the insects ; this view is erroneous, since no reduction of specific gravity with regard to the surrounding air can result from the air-sacs.

Reactions to Stimuli

All the behaviour of grasshoppers and locusts (as in other insects) is mainly composed of such movements as, on close study, prove to be direct reactions of the organism to certain external stimuli—that is, of *reflexes*. Combinations of separate reflex movements, which are often caused by several simultaneously-acting exciting agents, usually complicate the behaviour to such an extent that only careful analysis and experiments can elucidate the actual mechanism of a given act of the insect. The great majority of students of the behaviour of Acrididæ have worked (and many are still working) on a very different basis. Assuming that the behaviour is determined by complicated inherited instincts that are not, or scarcely at all, dependent on external factors, such authors, instead of analysing certain acts, have attempted simply to explain them in most cases on the ground of the advantages derived by the insect from them. As a result, there has accumulated a considerable amount of ingenious speculations on the utility and possible phylogenetic origin of a certain act, but the acts themselves and their mechanism remain practically unstudied. It is only quite recently that such attempts at explanation have given way to the much more laborious and useful work of detailed research into the behaviour of locusts. The results are, so far, very modest and require repeated checking, but it is perfectly clear that this is the only way to a real knowledge of the subject and to useful practical conclusions. Being firmly convinced that further studies in this direction must constitute the most important item in

research on locusts and grasshoppers, I will give a summary of the data obtained up till now.

Mechanical Stimuli.—The ACRIDIDÆ react in different ways to mechanical stimuli, according to where they are applied and to other conditions. Thus, if a grasshopper is laid on its back and its sternum is pressed, a temporary paralysis may be produced (Rabaud, 1919). The same result may be obtained in *Anacridium aegyptium* by pulling its antennæ. The duration of the paralysed condition depends on the temperature—at 13° C. it lasts 4–10 minutes, at higher temperatures it is shorter, while on a very hot day paralysis cannot be produced at all (Grassé, 1922).

Jumping, the movement most typical of the ACRIDIDÆ, is undoubtedly a reflex action, since the jerking movements of the hind legs, as in jumping, may be produced by touching the abdomen of an insect held by its elytra, from below along the median line ; in nature, the same reflex may result from rubbing the abdomen on the ground when crawling (Rabaud). Other stimuli, mostly unstudied, may also be responsible for the jumps, which differ in their energy in accordance with that of the stimuli. A gradual weakening of the reaction, when stimuli are repeated, is typical of reflex movements in general, and this may be observed in the jumping of ACRIDIDÆ, in which a paralytic condition of the hind legs is the usual result of repeatedly forced jumps.

Amongst mechanical stimuli, resulting in a jumping reflex, vibration of the air deserves special mention. Vayssière (1921) observed that an adult *Dociostaurus maroccanus* takes off (this act being nothing but a jump) when another individual flies above it ; a stone thrown so as to pass over a sitting insect does not produce the same reaction so that the insect seems to be able to distinguish the quality of the vibrations of the air, probably by means of the tympanal organs. A sudden approach to a sitting insect also results in a jump, unless it is done very quietly, without causing any vibration of the ground or air. There can be scarcely any doubt that the same reflex may be due to visual stimuli, but these are of secondary importance, since Lepiney (1928) found that blinded locusts respond to the approach, while normal ones put behind a glass do not. The whole problem presents an almost unexplored field for most interesting observations. When more data are accumulated, it will become possible to estimate the true significance of various stimuli that produce jumping. On the other hand, all current explanations of jumping, as an act useful for the preservation of the species, may be safely dropped as they explain nothing and do not in any way help the elucidation of this important element in the behaviour of the ACRIDIDÆ.

A very well-known reflex, peculiar to the ACRIDIDÆ, is autotomy, or throwing off the hind legs. It is usually produced by a pressure or tugging at the hind femur, but no detailed studies of this reflex have been made, and it is possible that it may be produced by stimuli applied to some other parts of the body also. Apart from mechanical factors, autotomy results from the electric excitation of the mesothoracic nervous ganglion, which seems to regulate this reflex (Grassé, 1923) ; autotomy under the influence of poisons (ACRIDIDÆ in the killing-bottle often throw off their legs), probably, also represents the

result of the excitation of the same ganglion. Autotomy in the hoppers occurs fairly often during the moults, when the hopper is for some reason unable to free its hind leg from the old skin (Nikolsky, 1925) ; in this case the connection between the mechanical stimulus and the reflex is obvious. Cases of voluntary autotomy, *i.e.* in the absence of a stimulus, that have been quoted in the literature seem to be very doubtful, and no exact and absolutely convincing experiment of this kind is known.

The anatomical mechanism of autotomy has not been sufficiently studied, but the rupture occurs always in the same place, at the junction of the femur and coxa, and bleeding is stopped by the contraction of a special membrane. The biological meaning of autotomy, according to the advocates of useful adaptations, is its use for the defence from the enemies—a grasshopper, caught by its hind leg, sacrifices it to save itself. However tempting this explanation may be, it cannot be accepted, at any rate, until it will be proved by direct and numerous observations that birds, for instance, catch grasshoppers by their hind legs ; against the main enemies of Acrididæ, *i.e.* their parasites, this method of defence is clearly useless. In any case, autotomy does not need explaining so much as studying by exact experimental methods.

Equally well known is another peculiarity of the Acrididæ, *viz.* the emission when taken in the hand of a drop of brown liquid (" molasses ") from the mouth. Rabaud (1915) studied this phenomenon, and his conclusion is that this is a reflex contraction of the stomach with regurgitation of its contents, caused by a pressure on the sides of mesothorax and metathorax, or on the front and middle femora. This reflex is also commonly explained as a defensive adaptation, causing an enemy to drop the captured grasshopper, but no direct observations of this kind are known to me, while it seems very doubtful whether a drop of the stomach contents of a grasshopper would produce such a startling effect on an animal that feeds on these insects.

Very interesting is the reflex of autohæmorrhage or bleeding from different parts of the body observed in several species. Vosseler (1902) studied this phenomenon in the North African species of *Oedaleus* in which the fluid comes out of the opening of a special gland under the pronotum (Fig. 43) ; there is no direct evidence (apart from histological structure) to show that this is actually a gland, and it seems more probable that the fluid emitted is simply blood, as happens in various long-horned grasshoppers. Nikolsky (1925) observed on one occasion a jet of fluid coming from under the pronotum of the hoppers of *Locusta migratoria ;* when taken in the hand, the hopper raises the hind part of its pronotum ; in the membrane between the pronotum and mesonotum appear two swellings, which then join together and burst, a jet of fluid up to 60 cm. in length being ejected from the opening ; the latter then closes, and the wound subsequently heals. No anatomical study of the larvæ was made, the fluid was not analysed, and the actual factors causing the phenomenon were not determined, but there seems to be no doubt that this is a reflex to a mechanical stimulus. Analogous phenomena are known in the African *Phymateus hildebrandti*, Bol., in which there are special gland-like structures at the base of the hind legs and a foaming fluid is emitted from them on the

insect being taken in the hand ; a regurgitation occurs at the same time, thus indicating the reflex character of the act (Pawlowsky, 1914). In the Indian *Aularches miliaris*, L., the fluid is emitted in large quantities from ten different points in the body (Hingston, 1927). The act is usually considered to be defensive, but direct observations on this point have never been made, and that grasshopper blood is distasteful to animals that feed on grasshoppers seems to be improbable. (A review of cases of autohæmorrhage in insects has been given recently by Hollande, 1926.)

Undoubtedly the process of emergence of the vermiform larva from the egg-pod to the surface of the ground must be referred to the category of reflex movements caused by mechanical stimuli. As already described, the vermiform movements continue only so long as the larva is subjected to pressure from the surrounding soil. The direction of its movement is obviously deter-

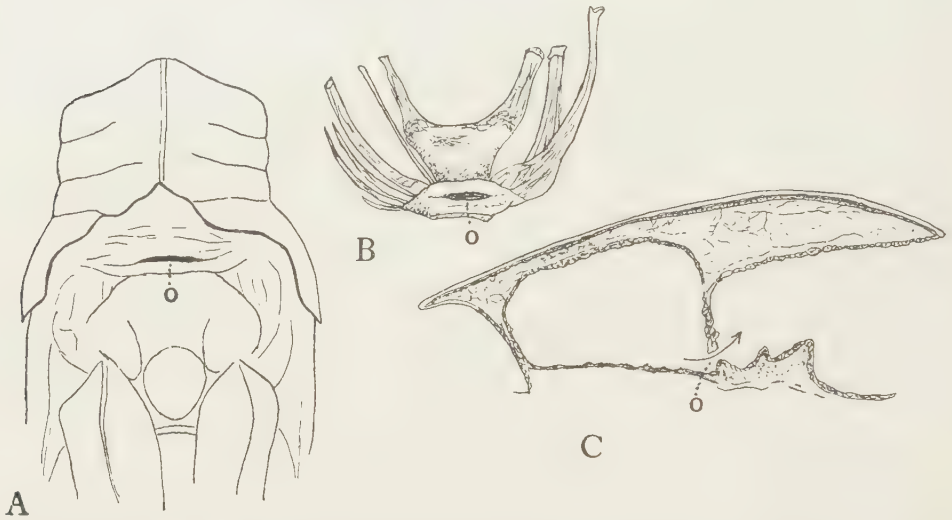

Fig. 43.—Fluid-emitting organ under the pronotum in *Oedaleus*.—A, dorsal view, with the hind portion of the pronotum removed.—B, the organ separated.—C, section of pronotum ; o, opening of the organ (after Vosseler).

mined by the force of gravity, which is, again, a mechanical stimulus. The same force plays some part in determining the direction of hoppers climbing plants for the night. Movement under the influence of gravity is usually called geotropism, and the vermiform larva must be considered to be negatively geotropic. Some traces of a positive geotropism were observed by La Baume (1918) in the larval bands of *Dociostaurus maroccanus* which tend to move downhill.

Influence of Temperature.—It is only quite recently that the influence of temperature on the behaviour of Acrididæ has been established, and it still remains insufficiently studied.

The temperature limits within which Acrididæ retain their vitality can be determined only from some disjointed data relating to several different species. The hoppers " of various species and stages " in the experiments by Antonov

(1922) were subjected to freezing at —5° C. for 30 minutes, with the result that their bodies became brittle ; when afterwards warmed in the sun, they very quickly thawed and recovered ; after being subjected to lower temperatures, down to —14° C., the percentage of individuals that recovered was smaller. In the more exact experiments of Parker (1924) with the hoppers of *Camnula pellucida*, those of the first and second stages survived freezing at —6° C. for 12 hours without any ill effects ; at —7° C. a certain proportion of them died, while 12 hours' freezing at —8° C. killed all of them.

The last-named author has also supplied some data on the upper temperature limit of life in the same species. When raising the temperature of the cage containing hoppers and adults by one degree in 5–10 minutes, he observed that at 50° C. a partial paralysis of the hind legs occurred and, in some individuals, a complete heat torpor ; at 54·5° the torpor became general, and only a few individuals survived for 5–10 minutes at 57·7°. Nikolsky (1918, 1925) records that the hoppers of the first stage of *Locusta migratoria* died on the bare surface of soil with a temperature of 57° C. ; in another experiment of his, when the surface temperature was 62° C., the hoppers of the first stage died after one minute's exposure, those of the second stage—after 1–2 minutes, of the third—after 3–7 minutes, and of the fourth—within 4–18 minutes.

However incomplete these data may be, and they probably must be corrected for the humidity which undoubtedly influences resistance to high temperatures, they show clearly that the temperature limits of life in the Acrididæ are wide and embrace about 60° C. But their activities, as evidenced by various kinds of movements, are far from being uniform at different temperatures within these wide limits.

Thus the hoppers of the Moroccan locust, according to Sviridenko (1924), enter a state of cold torpor at under 10° C., while in *Locusta migratoria* in the first stage heat torpor was recorded at 40° C. (Nikolsky, 1925) ; thus the limits of the active life are not very wide. Still narrower are the optimum limits of activity. The lower temperature limit when the hoppers begin to exhibit feeble movements have been determined by various authors with remarkable uniformity. My own very imperfect observations on *Locusta migratoria* (1921, 1923*a*) established that the hoppers in the morning begin to leave the plants where they passed the night when the temperature of the air reaches about 16° C. Numerous data accumulated by Nikolsky (1925) on the same species show that the first morning movements of the hoppers in the first stage begin at 12–13°, and that at 14–16·5° (at 20–22° in the older stages) they begin to crawl down from the plants. Parker (1924) determined the beginning of the active life of *Camnula pellucida* at 16·5° ; and Kiritchenko (1926) states that the hoppers of *Calliptamus italicus* become active when the temperature of the air reaches 15° C.

A further rise in temperature results in a progressive increase of energy of movement, but this goes on only up to a certain limit. In *Locusta migratoria* the mass movement of larval bands ceases when the temperature on the surface of the ground reaches 50–57° C. (Nikolsky, 1925), so that in this species the optimum conditions for activity are within the limits of 15–50° C. Still

narrower are the limits of optimum activity in *Calliptamus italicus* in which the mass movements of hoppers begin at 15° and stop when the air temperature reaches 25–26° C. (Kiritchenko, 1926). A very interesting experiment that deserves to be repeated with different species has been made by Parker (1924) with the hoppers of *Camnula pellucida*. A sheet of glass, covered with paper, was warmed in the centre from below by an electric lamp so that the temperature in the centre reached 60° C., and decreased toward the circumference ; the hoppers placed on the sheet arranged themselves after a few hours in a regular circle at the point where the temperature was 36·6–37·7° C. ; this experiment was repeated several times with the same result.

All the above data relating to the influence of temperature on the activity of ACRIDIDÆ, while clearly defining the importance of this factor in their behaviour, do not determine precisely how it acts. Direct observations on the action of temperature reveal that it has a twofold importance in regulating behaviour. First of all, there is no doubt that raising of the temperature results in the increased energy of reflex movements under various other stimuli. As an example may be quoted an observation by Nikolsky (1925), who found that the length of the jumps of hoppers greatly increased with a rise in temperature ; the latter also influenced the velocity of mass movements of the larval bands. Exact observations on the influence of temperature on the energy of various reflex movements are, however, lacking.

Perhaps more important is the direct action of temperature as a stimulus to movements. Field observations by various authors have established firmly that a great proportion of the movements of ACRIDIDÆ in a definite direction is due to positive thermotropism. Most convincing of all such observations are those on *Calliptamus italicus* by Kiritchenko (1926), who found that the movements of the hoppers climbing on to the plants or descending to the ground are invariably due to differences in the temperatures of the air and of the ground, the hoppers always exhibiting positive thermotropism ; when, however, the temperature approaches the upper limit of optimum conditions, the tropism is reversed and the hoppers become negatively thermotropic.

Exact laboratory studies of thermotropism in *Anacridium aegyptium* by Grassé (1922) fully support the results of field observations. In his experiments, a grasshopper placed in a cylindrical cage of wire netting moved towards the end of the cage where a hot plate was placed ; reaching the end, the insect stays there some time, then turns round and goes back, returning again to the warmth and again leaving it (Fig. 44). This experiment shows that positive thermotropism is liable to change when the body temperature of the insect becomes too high. I particularly insist on the importance in this case of the body temperature, since this must be the actual factor determining the physiological activities of the insect. Unfortunately, this side of the problem has never been studied, though we shall see later, when discussing the behaviour of swarming locusts, that with it is connected the solution of the main problems of mass migration as well as those of the periodicity of locust invasions.

Influence of Light.—The susceptibility of ACRIDIDÆ to light finding its

expression in movement towards its source, *i.e.* in the positive phototropism, has been repeatedly recorded by nearly all authors on the bionomics of these insects.

As early as the intermediate moult, light plays the rôle of a stimulus (see p. 43). Immediately after that moult, the inclination of hoppers to move towards the source of light is very marked, the hoppers always placing them-

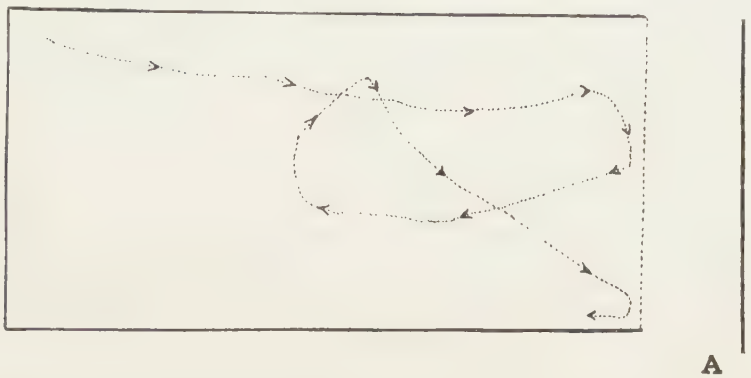

Fig. 44.—An experiment with thermotropism in *Anacridium aegyptium*.—A, heated plate.—Dotted line inside the cage indicates the route traversed by the insect (after Grassé).

selves on the best lighted side of a cage if bred in captivity. The hoppers of the Moroccan locust on cloudy days collect on a white sheet placed on the ground, but if the day is very bright they avoid white, their phototropism apparently changing (Sviridenko, 1924). Artificial light at night attracts various species of Acrididæ, and in Transcaspia I used to collect in this way a number of species and individuals (see also p. 89).

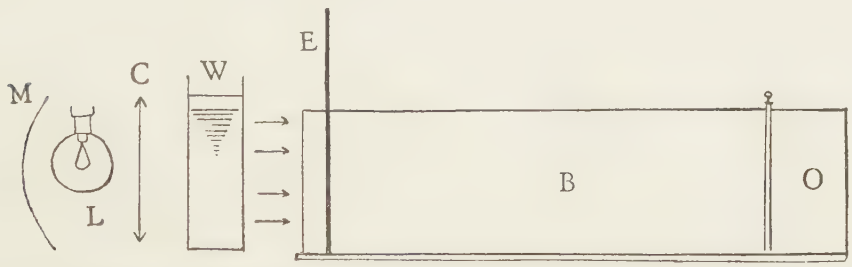

Fig. 45.—Apparatus for experiments with phototropism.—M, concave mirror; L, lamp; C, bi-convex lens; W, parallel-sided glass jar with water to absorb the heat rays; E, non-transparent screen which may be pulled out upwards; B, box for the insects; O, section of the box where the insects are kept before the experiment (after Grassé).

Experimental studies of the phototropism in Acrididæ have been made by Grassé (1922, 1923) on three different species with the same result (Fig. 45). The velocity of reaction to the stimulus of light varies in different individuals of the same species and also depends on the quality of the source of light, the most rapid reaction being towards the direct rays of the sun (heliotropism), while diffused light acts very slowly. Phototropism is also exhibited by individuals that have been partially blinded by covering one eye, a lateral

ocellus and the median ocellus with varnish ; no reaction to light is observed when all the eyes and ocelli are varnished.

It would be not out of place to discuss here the part played by vision in the behaviour of ACRIDIDÆ. There is no doubt that vision is fairly good in these insects, but it seems that they mainly see moving objects. One can cautiously approach a sitting grasshopper without disturbing it, but one sudden movement of the arm is sufficient to send it flying. The fact that the sudden movement of an object in the field of vision of a hopper results almost invariably in a reflex jump is specially worth remembering, since we shall see later how important it is in connection with the behaviour of larval bands.

The Influence of Chemical Factors.—The attraction of locusts by certain chemicals (in poisoned baits) has found such an enormous field of practical application that one would naturally expect that the theoretical foundations of such a method had been thoroughly well investigated. This, however, is not the case, and our actual knowledge of the influence of various chemicals on the behaviour of ACRIDIDÆ is incredibly small.

To begin with, we do not know how the stimuli excited by chemicals are received by the insects ; this problem, however, has already been discussed (see p. 24).

Apart from the question of selection of food plants, which we shall study later (p. 73), we may now point out only one chemical combination towards which the ACRIDIDÆ nearly always exhibit a positive chemotropism, this being water. Nikolsky (1925) especially has very clearly shown that the attraction of hoppers by various plants, that are not usually eaten by them, is due to their hydrotropism. The importance of water in the physiology of ACRIDIDÆ is very convincingly demonstrated by the experiments of Bodine (1921), who found that during forced fasting the hoppers rapidly lose in weight, the loss being mainly due to the reduction of the percentage of water in the body. This means that hungry hoppers must invariably also be thirsty, and they are therefore attracted by moisture in any form.

Amongst other substances generally attractive to ACRIDIDÆ, amyl acetate may be mentioned (Parker, 1924), while later, when discussing the method of control by poisoned baits, we shall have an opportunity of learning a little about the relative attractiveness of several others. All this information is, however, entirely empirical, and a serious study of the chemotropic responses of ACRIDIDÆ has not even been begun. The main reason for neglecting this highly important question is that it is first of all a chemical problem, and the vast majority of entomologists are very poor chemists.

Interaction of Various Factors.—Under natural conditions it can scarcely be expected that a certain factor would influence the behaviour of the insect without the interference of other factors. Light, temperature, and mechanical stimuli all act on the organism more or less simultaneously, and the result is due to their combined action. Therefore, to understand the behaviour of ACRIDIDÆ under natural conditions, we must study their reactions not only to different separate factors, but also to their combinations. Observations in

this direction are very meagre, but they demonstrate clearly the importance of this view.

It has already been stated above (p. 70) that the energy of a jump increases with an increase in temperature ; in other words, the energy of the reflex action caused by a mechanical stimulus depends on temperature. This is corroborated by the fact that a paralytic condition in *Anacridium aegyptium* can be obtained by pulling the antennæ only at certain low temperatures, but not when the temperature is high. Phototropism in the same species also depends on the temperature : at 12° C. it is very strongly positively phototropic, at 25° much less so, and at 30° its phototropism becomes very feeble (Grassé, 1922).

Feeding Habits

The enormous voracity of locusts and their ability to devour absolutely everything thay may meet on their wanderings has become proverbial with nearly all peoples, and these habits are often considered to be firmly established and not deserving closer study. The latter, however, reveals many new and unexpected facts, which tend to throw considerable doubts on the correctness of the above assumptions.

The normal food of the Acrididæ comprises the green parts of various higher (flowering) plants, and only the Tetrigidæ feed partly or wholly on lichens and the microscopic algæ found in mud or in soil rich in humus (Hancock, 1898). Feeding on animal food occurs only exceptionally, and we shall return to this point later.

As regards the selection of food-plants, various species exhibit a different degree of range in their tastes. It would be difficult to point out with absolute certainty any *monophagous* species, *i.e.* one feeding only on a certain species of plant, but it seems that the Caspian *Derycoris tibialis*, Pall., feeds, both in the larval and adult stage, only on *Anabasis aphylla*, a thick-leaved halophilous plant. We know absolutely nothing concerning the food of the vast majority of species, not known as pests. Judging from the relative abundance of species and individuals of Acrididæ in grassland habitats, there is a definite preference for the Graminaceæ, and this is corroborated by observations on most, but not all, injurious species. Trees and shrubs attract but very few species, and the Acridid population of such areas is poor ; direct evidence on species feeding on them exclusively, or practically so, is restricted only to very few, such as *Anacridium aegyptium*, *A. melanorhodon*, Walk. (Johnston, 1924), some American species of *Melanoplus*, etc.

Within the group of Graminaceous plants, the species that feed on them exhibit further discrimination. Thus *Locusta migratoria*, which is usually considered " omnivorous," is in fact closely connected in its feeding habits with the reed, *Phragmites communis*, and only in its absence does it attack other grasses, while other plants serve as food only when no Graminaceæ are available. Millet and allied plants are, generally speaking, very little eaten by Acrididæ, but the Indian Jola grasshopper (*Colemania sphenarioides*) exhibits a special preference for plants of this group (Coleman, 1911).

To demonstrate still more convincingly how strongly the tastes of various

species may differ, it may be pointed out that *Locusta migratoria* eats all leguminous plants very reluctantly, while *Dociostaurus maroccanus* prefers them to many others; both these species avoid *Artemisia*, which is the favourite food of *Calliptamus italicus*.

These food-preferences are observed, however, only when there is a possibility of choice, but when the preferred plants are absent, the same species may feed on many others, not even avoiding those that are directly poisonous. Thus *Dociostaurus maroccanus* in Asia Minor, when there is no other vegetation, feeds on *Peganum harmala* with fatal results (La Baume, 1918). Observations in the laboratory show that some of the plants readily eaten may also be harmful; for instance, a high mortality results from the feeding of hoppers on young oats, while adults raised on these do not develop genital products (Carothers, 1913; Maltsev, 1914).

It is a very interesting fact that in some species the number of plants used for food increases with the development of the hoppers. The hoppers of the Moroccan locust in Transcaucasia in the first stage feed almost exclusively on the grass, *Poa bulbosa*, but with each moult the number of food-plants increases (Sviridenko, 1924). Analogous facts were observed in *Locusta migratoria* by Kulagin (1922), who accounted for them by the greater development in the hoppers of the two first stages of the nerve (taste) endings as compared with the later stages.

All this tends to show that popular opinion as to the omnivorous habits of Acrididæ is subject to numerous limitations. It is true that for practically each of the injurious species there is a very long list of plants, on which it has been recorded as feeding at various times and in various countries. Such lists, however, cannot be accepted as actual lists of food-plants of the species, since even the occasional nibbling of a plant is usually recorded as feeding, while very often injuries of this kind are caused by the insects seeking water, not food. A typical example of this may be commonly observed in the injuries caused by migrating swarms of *Locusta migratoria*, which often settle on trees and nibble the stalks of leaves so that the latter drop, but are not eaten. Nikolsky (1925), who drew special attention to this fact, records some still more striking illustration of the water requirements of locusts, when he describes swarms settling down at the edge of water, or destruction, by a swarm, of damp washing hung on lines to dry; in the latter case such clothing as was already dry remained intact.

It seems reasonable to suggest that the same want of water must be responsible for the cases of locusts devouring the crushed bodies of their own species. This cannibalism on the part of the hoppers is often quoted in the literature, and some authors are even inclined to regard it as an important factor in reducing the numbers of locusts; this is quite groundless since only wounded or dead hoppers are thus attacked, and the proportion of those eaten is negligible. Attempts were made by Nikolsky (1925) to breed *Locusta migratoria* on animal food (larvæ of *Melolontha* and *Potosia* or dead hoppers), but without success; the hoppers ate the food offered, but failed to moult and died.

The importance of water to ACRIDIDÆ has been clearly demonstrated by experiments with fasting. Speaking generally, hoppers can remain without food for a considerable time—those of the Moroccan locust in the first stage up to six days (Sviridenko, 1924); *Locusta migratoria* in the first stage—up to $7\frac{1}{2}$ days, of the second, third, and fourth stage—up to 6 days, in the fifth stage—9 days, and the adult up to $10\frac{1}{2}$ days; in all cases the insects received neither food nor water (Michelson, 1922). Bodine (1921) in his very exact and detailed experiments found that the adult *Melanoplus femur-rubrum* can survive complete fasting, without water, for 73 hours, while without food, but with water, it can live for 144 hours; for *M. differentialis* the respective figures are 96 and 172 hours. A study of the changes in the body-weight and in the percentage of water during fasting, made by the same author, showed that the loss in weight may be very great, reaching 20–25 per cent. at the moment of death, but the loss is due mainly to the rapid decrease in the water-content, not to the expenditure of dry matter.

The very important and interesting question of the quantity of food required for the development of a single individual remains practically unstudied, though there are some data relating to two species.

Lebedev (1923) bred in the laboratory one individual of *Locusta migratoria*, with a record of the quantity of food taken during each stage of development. The results are as follows:

Stage.	Average weight of the insect.	Weight of food eaten.
I	0·025 gr.	0·25 gr.
II	0·05 ,,	0·6 ,,
III	0·12 ,,	1·64 ,,
IV	0·32 ,,	7·3 ,,
V	1·35 ,,	16·3 ,,
Adult	—	241·3 ,,
	Total	267·39 ,,

The degree of exactitude of these data is not clear, since the author only states that the records were based on measurements of the surface of the consumed portions of the leaves, but does not describe the method by which these figures were used in calculating the weight of the food. The figure for the adult is obtained from the average for 13 days and on the theoretical assumption that the adult lives for 60 days and feeds at a constant rate, which is not in accordance with the facts. In any case, the figures illustrate how rapidly the amount of the food eaten increases with the growth of the hoppers: particularly interesting is the fact that the relative quantity of food, as compared with the weight of the hopper (included in the table from Nikolsky, 1925), increases rapidly in each subsequent stage, the hopper of the first stage consuming ten times its own weight and that of the fourth stage more than twenty times its weight. Since the hopper in Lebedev's experiment passed nearly eight full days in the fourth stage, its food consumption in a day was $2\frac{1}{2}$ times its own weight.

Such relatively large amounts of food eaten by the hoppers indicate that it must be very incompletely digested and absorbed. Unfortunately, there are no data on the chemistry of nutrition in ACRIDIDÆ, but their excreta consist

of vegetable remains scarcely digested, and the pieces of leaves found in them do not even lose their structure.

Observations by Valova (1924) on the feeding habits of *Chorthippus scalaris* in the laboratory showed that a sudden increase in the quantity of consumed food occurs after the hopper has entered the second stage, during which it consumes daily, on an average, twice as much as in the first stage ; during the next stages, there is a regular increase in the amount of food consumed both daily and during the whole stage, but the difference between the two successive stages is never so great as between the first two. During the adult stage, half again as much food is consumed as during all the larval stages.

The data on the conditions of feeding are very interesting theoretically and are also important in connection with control. A special position in this respect is occupied by the hoppers of the first stage, which for a long time were supposed not to feed at all, or to feed only on dew. As a matter of fact, there is only a more or less prolonged period after the intermediate moult during which the hopper does not take any food ; this period in *Locusta migratoria* varies from 12 to 24 hours (Lebedev, 1923 ; Nikolsky, 1925), while in *Chorthippus scalaris* it averages 16 hours 24 minutes (Valova, *l.c.*). Very thorough observations by Valova showed that only in exceptional cases do the hoppers begin to take food on the day of emergence ; as a rule, feeding begins only on the next morning, and the length of this fasting period does not depend either on the meteorological conditions or on the time of the day when the hopper emerged, while the beginning of feeding on the next day is wholly connected with the action of the direct rays of the sun. The physiological reason for this fasting during the first day consists, according to Kulagin (1922), in the presence in the stomach of the young hoppers of the remains of the egg-yolk, and only after this is digested does the hopper begin to feel hunger ; if this is so, there is no reason to call this period fasting. Nikolsky (1925) is inclined to see the reason for the hopper abstaining from food in the fact that its stomach just after emergence is still filled with air, swallowed during the intermediate moult, and that its mouth-parts harden only some time after the moult.

Temperature is a very important factor affecting feeding ; its fluctuations are particularly strongly reflected in the amount of food taken by the hoppers during the first two stages, when a drop in temperature immediately causes a reduction of it. During the later stages, this is less noticeable (Valova, *l.c.*).

According to the very exact observations of Parker (1924), the feeding of the adults of *Camnula pellucida* on plants occurs, as a rule, at temperatures not under 20° C., and ceases again at 32° C. ; on baits, feeding begins at 18–20°, is most marked at 21·6–25°, and gradually diminishes at higher temperatures. The temperature limits for the feeding of hoppers of *Locusta migratoria* are very close to those for *Camnula*, since Nikolsky (1925) observed the beginning of feeding at 18·5°, and found that it was still possible at 34–35·5° C.

The rôle of temperature in increasing the amount of food consumed consists, obviously, in the acceleration of all physiological processes, but the

cessation of feeding at high temperatures must be due to the direct effects of heat, which either compels the hopper to move or results in heat torpor.

Other meteorological conditions, apart from temperature, also influence the feeding habits. Valova (*l.c.*) quotes an observation that on two consecutive days, the first of which was rainy and the second fine, there was a sharp increase in the amount of food taken on the second day. The insects were in the laboratory, so that the direct effect of rain was excluded, and the reason for the change might have been either in the humidity of the air, or in the influence of light on the general activity of the insects.

Amongst the physiological factors of feeding we have already discussed the possible reason for the "fasting" of the recently emerged hoppers. A very important factor of this kind is presented by the moults. Valova has established that the hoppers do not take any food for a considerable period both just before and just after each moult; the average period of fasting is 27 hours 20 minutes at the first moult, 32 hours 30 minutes at the second, 42 hours 40 minutes at the third, and 61 hours at the fourth, so that during the whole development as much as 163 hours are passed in fasting in connection with moults. The complete interruption in feeding does not occur suddenly, but the amount of food consumed begins to decrease four days before a moult and does not return to the normal until three days after it. The physiological reasons for this phenomenon are obscure, since our general knowledge of the physiology of feeding of the ACRIDIDÆ is very slight.

THE BEHAVIOUR OF GREGARIOUS LOCUSTS

Having summarised the existing data on the factors that produce certain actions in the ACRIDIDÆ, such as movement, feeding, etc., we may now pass to a discussion of their behaviour, which must be regarded as a combination of various movements. Since the behaviour of ACRIDIDÆ in the hopper stage differs substantially from that of the adults, it seems more convenient to discuss them separately.

Particularly interesting and, at the same time, better studied is the behaviour of the gregarious species, or locusts proper, and I will begin with them.

Gregariousness.—All typical locusts are characterised by the inclination of their hoppers to live in close communities from the time of hatching up to the adult stage; these communities are sometimes called swarms, but, to avoid any possible confusion, I prefer to reserve this term for the adult swarms only, and to call the accumulations of hoppers—*bands*.

Formation of the bands depends on the presence in the gregarious species of a special biological faculty, which compels the hoppers (*a*) to keep close to each other, and (*b*) to repeat each other's movements. These two component parts of the "gregarious instinct," as it is usually called, are, most probably, simple reflexes, though an exact analytical study of their nature has not even begun.

The first component, inclination of the hoppers to form dense accumulations, is a very well-known fact, but this inclination varies in its intensity even

in the same species. Thus the hoppers that are preparing to moult become less gregarious, and may even temporarily lose all connection with a band. As to whether it is the visual, or olfactory, or some other sense that is behind this faculty, we know absolutely nothing, and there is here a great field open for interesting investigations.

The second component of the behaviour of gregarious species is the inclination of hoppers to repeat the movements of their nearest neighbours. Owing to it, the jump of a hopper causes the jumps of several others, apparently as a reflex either to the mechanical excitation (jolt, vibration of air, or of the ground), or to the visual one. This reflex, causing an animal to pursue a swiftly moving object, is very common with many animals, but there seem to be no investigations bearing on it. The only theoretical explanation offered for it is that by Loeb (Forced Movements, Tropisms and Animal Conduct ; 1918 ; p. 131). This author believes that the movement of the images of surrounding objects on the retina causes reflex movements that aim at stopping this movement by moving the eye (*i.e.* the whole animal) in the same direction as the objects move. In our case, then, a movement of one hopper in a given direction causes reflex movements on the part of its nearest neighbours in the same direction, and the movement spreads in this way through the whole band, provided that the other conditions (especially temperature) make the hoppers sufficiently excitable.

This explanation of gregariousness and the mass movement of locust hoppers may serve as a working hypothesis, and it shows the lines of future investigations of the nature of mass movements.

Formation of Bands.—Owing to the fact that the egg-pods of gregarious species are laid in more or less dense groups, the hoppers from the very beginning of their free life come into close contact with each other. As a result of their inclination to segregate, they form small dense primary bands very soon after the intermediate moult ; these appear like blackish spots scattered over the area, where the hoppers have emerged (Plate VI, Fig. 2). In the actual formation of these bands a very important part belongs also to the thermotropism and phototropism of the hoppers, which all try to occupy the optimum position with regard to light and warmth. According to observations by La Baume (1918) and Sviridenko (1924), the hoppers of the Moroccan locust form primary bands, if the day is bright and hot, on bare spots of ground, on hillocks, stones (Plate VI, Fig. 3), and similar places under the direct influence of the sun. La Baume believes that the formation of bands in such places occurs automatically ; a crawling hopper stops where it finds the optimum temperature of the surface (compare experiments by Parker, described on p. 70) ; other hoppers stop at the same places, partly for the same reason, partly owing to gregarious habit, and a band results.

In cool and wintry weather, according to La Baume, the bands form as a result of the hoppers seeking shelter behind stones, in small hollows in the ground, amongst plants, etc., again owing to their positive thermotropism. In this case (as perhaps in many others) an important part belongs not only to the temperature of the air and of the surface of the ground, but also to the

animal heat of the hoppers themselves. The importance of this factor has been pointed out by Nikolsky (1925), who, however, regarded the problem from a somewhat different angle, and believed that " the grouping of the hoppers into the primary bands must be considered a remarkable adaptation for the utilisation of the sun's rays and animal heat." There is no doubt that a better utilisation of heat is realised in close segregations, but this is not the object of the process so much as a result of the positive thermotropism of the hoppers. Animal heat must in this case play its part in the raising of the temperature of the whole band to the optimum, though actual observations on this point are lacking. To what extent the formation of the primary bands depends on visual impressions, it is impossible to say without special experiments, which, incidentally, should not be difficult to arrange by varnishing the eyes of experimental hoppers.

Further development of the primary bands and formation of the larger bands will be made clear later, since this occurs in connection with the movements of bands, which we will now discuss.

Movements of Bands.—The daily regime of the behaviour of the hoppers during the first days of their life is very simple. A great portion of the day is spent by the primary bands in basking in the sunlight as described above ; at night the hoppers either crawl under stones or climb on to plants, forming dense clusters on them. Crawling under stones, etc., represents only a repetition of the similar phenomenon observed on cold days (see above), while the habit of climbing on to plants has been very insufficiently studied with regard to the hoppers of the first stage, and it is more convenient to discuss this process later. During the first days, as we know, the hoppers feed very little, and there is no adequate information as to the conditions of their feeding.

Towards the end of the first stage and during the next stages, the daily regime of the bands, in normal weather conditions, becomes very regular and may be outlined as follows :

The night is passed on plants in dense bands, which are extremely conspicuous on the background of the vegetation owing to their blackish general colour ; during the night the hoppers are in the state of torpor, caused by the cold (Plate VII). In the morning, under the influence of the first rays of the sun, the first movements of the hoppers become apparent ; the first to move are those that are under the direct rays of the sun, and they shift their position on the plants to get the fullest advantage from it. These movements are undoubtedly simple reflexes, but it remains somewhat uncertain whether they are stimulated by the heat of the rays or by the light of the sun, *i.e.* whether the reaction is thermotropic or phototropic.

A further rise in the temperature partly causes feeding and partly climbing or hopping from the plants on to the ground, where they form close groups on the best lighted and warmed places, as already described. The descent of hoppers from the plants can be satisfactorily explained by their positive thermotropism, because the data collected by Nikolsky (1925) and by Kiritchenko (1926) show that the temperature on the ground rises in the morning more rapidly than on the plants where the hoppers are, and they simply move towards

the higher temperature ; this movement, however, can begin only when the body temperature of the hoppers becomes sufficiently high to overcome their torpor.

The actual figures relating to the temperatures at which the morning descent takes place are known only for two species of locusts. Nikolsky (1925) found that these temperatures are different for the different stages of the hoppers of *Locusta migratoria ;* hoppers of the first stage descending when the temperature of the air is 14–15° C., those of the second at 15°, of the third at 16°, of the fourth at 17° and higher, and of the fifth stage at 21–22°, that is, the older the hoppers, the higher the temperature required to produce the same effect.

Kiritchenko (*l.c.*), in describing his observations on *Calliptamus italicus*, says that in this species the mass descent of hoppers occurs when the temperature on the plants reaches about 15° C. (critical point) and the temperature on the surface of the ground is about 20–25°.

With regard to the morning feeding of hoppers, there is some difference of opinion. According to my own observations, the hoppers of *Locusta migratoria* feed before descending from the plants, but Nikolsky states that this only occurs occasionally, and that normally the hoppers begin to take food after descending and passing some time in dense groups on the ground. Kiritchenko made analogous observations on the behaviour of *Calliptamus italicus*, and there is, apparently, no definite general rule on this point, but the time of feeding depends on the actual conditions of temperature (and probably of moisture) at different moments ; exact observations bearing on the problem are urgently wanted, as it has an important bearing on the question of control by spraying.

The higher the sun rises above the horizon, the more active the hoppers become. They begin to crawl to and fro, to make jumps, and as a result, instead of several small, but very dense, groups, one larger, but less dense, band is formed. Interesting observations by Moritz-Romanova (1925) show that the surface covered by a band after this scattering is sometimes three times that occupied by it at night.

This dispersal of the morning groups is in a very close relation with temperature conditions ; Kiritchenko observed that on cool days it does not happen at all, and that the hoppers pass all day in dense groups, which begin to disperse when the temperature on the surface rise above 30° C., and that of the air above 21° C. Nikolsky states that the morning groups of *Locusta migratoria* in the first stage disperse at a ground temperature 25–28° C., and in the third stage only at 35–38°. Here again a stronger stimulus is necessary to produce the same effect in the older hoppers than in the young ones ; this may be explained if we assume that the process of dispersal is a result of excitability of hoppers caused by a rise in the body temperature ; and it is obvious that more heat is necessary to raise this temperature to the same point in larger insects than in small ones.

The next stage in the behaviour of bands is their migration, or, as I prefer to call it, owing to its somewhat irregular and obviously aimless character, wandering. Its beginning is, again, connected with a further rise in the

temperature of the environment (air and surface of the ground) and probably of the body temperature of the hoppers. Bands of hoppers of *Locusta migratoria* begin to move when the temperature on the surface reaches 31·5–38° C., according to the stage of the hoppers (Nikolsky, *l.c.*) ; for the Moroccan locust, Sviridenko (1924) quotes only the temperature of the air corresponding to the beginning of mass movement, as 23·5–27° C. ; *Calliptamus italicus*, according to Kiritchenko, begins to wander when the temperature on the surface of the ground rises above 30° C.

The beginning of the mass wandering of hoppers in bands may be described as follows. Some of the hoppers become restless, make irregular small jumps, which cause reflex jumps on the part of others, and in this way some centres of movement arise in different sections of the band ; movement is at first irregular, but soon a common direction is found, owing to the inclination of hoppers to move parallel to each other (see above). This common direction of movement of each band is, therefore, determined by accidental conditions, and separate bands may begin to move in different directions. In some cases, however, the direction of movement of individual hoppers and, consequently, of their bands is determined by certain external factors ; thus, for instance,

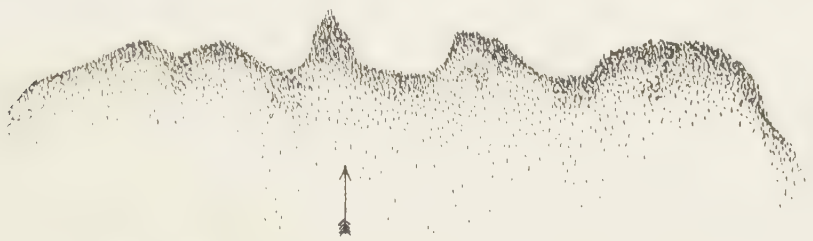

Fig. 46.—A band of locust hoppers on the march (original).

bands of the Moroccan locust very often march downhill. Siazov (1913) explained this fact by the assumption that the bands move towards the richer green grass of the valleys, but La Baume (1918) makes the much more reasonable suggestion that this is only a manifestation of positive geotropism. All attempts to connect the direction of movement with the cardinal points, the position of the sun, or the direction of the wind, have given so far most contradictory results, and none of these factors are likely to play any serious part in determining the direction of movement, though they may perhaps influence it to some extent.

A band once started on its march positively cannot stop, since the hoppers, owing to their gregariousness, strive to keep as close as possible to each other and produce continuous mutual stimuli resulting in jumps and crawling. The band therefore *must move*, regardless of where this movement may lead it, and the result is the blind march of masses of hoppers.

The bands usually move, not in dense masses, but in a formation with a broad but not very deep front (Fig. 46). In front the band is defined very sharply, the first rows of the hoppers being particularly dense, while behind they become less so. The shape of the bands varies greatly in connection

with purely accidental causes, such as the unevenness of the surface, varying density of vegetation, etc.

The described formation of bands can be preserved in its typical form only when the ground traversed is flat and the vegetation sparse. If the surface is very uneven, the formation suffers considerable modifications, simply because the movement is directed mainly along the lines of the least resistance. Thus, in dense reeds the bands of *Locusta migratoria* usually wander in narrow and long columns along the clear paths made by cattle (Nikolsky, 1925).

When two bands moving in different directions meet, they usually form one large band that continues to move in the direction of the larger of the two ; there is, of course, no general rule for these cases, except that it is seldom possible for each band to continue on its own way. As a result of such chance encounters and of the fusion of bands, enormously large bands, stretching for miles and blindly marching along, are formed ; picturesque descriptions of such great bands of hoppers abound in various books of travel. The relentless march of such masses of hoppers, regardless of obstacles, creates an impression of some dark purpose, of a movement towards an objective, and has led to numerous more or less fantastic explanations of the causes of movement based on the imagination of the observer and not on the facts. To this problem, however, we will return later.

Obstacles to the moving bands, in fact, do not seem to exist ; they pass over hillocks and boulders ; holes and ditches on the ground are filled with the bodies of the first coming hoppers, and their comrades pass over them as if over level ground ; absolutely insurmountable obstacles, such as smooth vertical walls, cause only an alteration in the direction of movement ; across canals and streams the bands swim to the other side and continue their march. This crossing of streams and even of broad rivers has nothing extraordinary in it, as the hoppers enter the water, of course, without any understanding what is before them, while swimming itself consists, as we know, of the same movements as marching.

Stopping of Bands.—This is possible only with a change in the conditions that make the movement possible, *i.e.* in temperature. Indeed, movement becomes more energetic and rapid with a rise in the temperature, owing to the increase of the length of reflex jumps, and slower when the temperature begins to drop towards evening. When it drops to a certain point, usually corresponding to that at which the movement begins in the morning, the bands stop gradually.

Sometimes the bands stop in the middle of the day, when the temperature rises so high that heat torpor overcomes the hoppers. In very hot countries this midday interruption of wanderings is, accordingly, a normal occurrence, and the hoppers usually seek shelter from the sun under plants, clods, stones, etc.

The evening stoppage of the bands is followed by climbing the plants and feeding (Plate I, Fig. 2). According to Nikolsky, this begins when the temperature of the air becomes higher than that on the ground, so that the hoppers climb under the influence of positive thermotropism. Kiritchenko, however, on the ground of very exact observations, states that the temperature on the

ground during the ascent of hoppers is usually the same as that of the air, or even actually higher; he thinks that the ascent is caused by positive phototropism of the hoppers, which at first concentrate on the spots of ground lighted by the sun, and when the latter goes down, they climb to catch its last rays. The movements of hoppers on the plants become less and less energetic, gradually die down, and the insects pass into the state of cold torpor, in which the night is passed.

Such is the general scheme of the daily movements of bands. Since all the details of the scheme depend entirely on the external conditions, it is natural to expect that any fluctuations of weather must alter or even destroy the regularity of the scheme, and this actually happens. If the weather is cool, the bands may pass the whole day on the plants, while a sudden drop in the temperature of a warm day results in the stopping of movement of the bands and in the ascent of hoppers on to plants. Temporary stoppages of bands may be observed even if the sun is obscured for a short time by a cloud, but in this case, the stoppage is caused not by a drop in the temperature, which cannot be sufficient, but by a sudden change in the intensity of light, which in all positively heliotropic animals produces a sharp reaction.

Causes of Mass Movements.—The problem of the causes which induce hoppers of gregarious species to undertake mass wanderings has been much more discussed in the literature than it has been actually studied.

The first suggestion, which naturally occurs at the sight of the moving masses of locusts, is that they move in search of food and that the beginning of the movement must be connected with the shortage of food supplies on the breeding grounds. Some of the older authors have already recorded observations that bands of locusts sometimes march past the best food possible without paying any attention to it, and Nikolsky in a series of investigations established quite definitely that the mass wanderings of hoppers of *Locusta migratoria* have nothing to do with the quest for food. Indeed, it is sufficient to observe the wandering bands for a single day to become convinced that to explain their movements on the ground of hunger is absurd. The morning descent of the hoppers from their food-plants to the ground is ample evidence that they are not driven by hunger. Later in the day the bands wander without any relation to food, often leaving rich vegetation to enter the bare desert. When a band is well on the move, it does not stop when it encounters suitable food, but a drop in the temperature automatically results in a stop, whether food is present or not. It is true that temporary cessation of movement in order to feed may be occasionally observed (especially in the Moroccan locust), but this happens only with hungry hoppers, which have passed the previous night on inedible vegetation; such stoppages are never prolonged, and after the acute hunger is appeased, the hoppers resume their march—very often away from the food. All this proves most categorically that the explanation of movement on the grounds of hunger must be rejected.

On the other hand, the connection between the temperature and other external conditions and movement is so very obvious that there is actually

no need to invent other explanations, and we need only try and analyse this connection more closely.

The part played by the temperature in this case may be twofold. Firstly, the experiments by Grassé (1922; see above, p. 70) have proved conclusively that the ACRIDIDÆ react towards a rise in temperature by making movements; still more definite results in the same direction were obtained by Parker (1924; see above, p. 70). The movements of hoppers thus represent a direct reaction to the rise in temperature of their body, while contact with the hot surface of the ground produces supplementary stimuli. A further increase of the nervous tension in the band is caused by the mutual excitations of the hoppers; Grassé in one of his interesting experiments (1923) has shown that reflex reactions of ACRIDIDÆ, even of the non-gregarious species, are more energetic if several individuals are subjected to the experiment together than in the case of a single insect. This condition is expressed in a band in the highest possible degree, while a high temperature, apart from its direct influence, also contributes to an increase in the excitability of the hoppers. All these conditions acting together must inevitably result in a strong increase of the nervous tension in the band, and this tension can find its expression only in a mass movement. The direction of the latter cannot be determined by the position of the source of warmth, since the whole environment has the same temperature and the general direction of the march is, therefore, quite fortuitous, as we have already shown.

All this needs considerable elaboration of details, but it is abundantly clear that the key to the elucidation of the whole problem of wandering in the hopper stage can be found only in the study of fluctuations of the body temperature of the insects in connection with the external conditions. Collateral evidence of the importance of the body temperature on the behaviour of hoppers may be seen in the coloration of the hoppers of gregarious species, in which black pigment always plays an outstanding part. This dark pigmentation inevitably causes an increased absorption of the heat rays and an increase in the body temperature; Buxton (1924) measured the body temperature of two colour forms of a Palestine grasshopper, *Calliptamus coelesyriensis*, and found that in the black form it was 4–5° C. higher than in the buff individuals under the same conditions. An analogous phenomenon of the increased absorption of heat should take place in the hoppers of gregarious species, and their "swarming coloration," as we have called it (see p. 49), must be to a certain degree responsible for their wanderings. On the other hand, these daily wanderings of hoppers cannot fail to produce some effect on their whole physiology, and we shall see later how this can influence still greater problems of the life of the species.

A study of the factors and of the mechanism of the mass wanderings of hoppers in all their details is thus obviously one of the most vital problems before entomologists, but it must be clearly understood that this is a purely physiological problem, and that it must be studied by the exact methods of experimental physiology; if possible, by physiologists or with their co-operation. At the same time, it must be hoped that the evidence collected on the

preceding pages will bring to an end the waste of time and energy expended on explanations as to how the " instinct of wandering " originated and why it is " useful " to the species ; all these suggestions may be ingenious, but they do not increase our knowledge by a single fact, and serve merely to obscure the only hopeful line of research.

Behaviour of Flying Swarms

The acquirement of wings by the hoppers of gregarious species results in some changes in the behaviour of the insects, though not so suddenly as might be supposed. At first, when only single, winged individuals appear in the larval bands, they behave in the same way as the hoppers, and even take part in the wanderings of bands, moving " on foot " without using their wings. With regard to the Moroccan locust, La Baume (1918) states that this method of movement may be observed even after all the hoppers in a band have become adult, and the band for some time continues the same life as when it was composed of hoppers. In *Locusta migratoria* this is not so, and for the Moroccan locust Sviridenko (1924) describes how the swarms disperse soon after the final moult, which indicates a lowering of the gregarious impulses. At the same time, all other stimuli produce less response in the adult than in the hoppers. According to Dampf (1925), the recently moulted adults of the Mexican *Schistocerca paranensis* are not easily frightened, *i.e.* their response to stimuli is low. A cessation of the wanderings and the habit of spending whole days quietly on plants seem to indicate that the responses to temperature influences are also depressed.

The first attempts to use the wings for flight may not be observed for some days after the moult, perhaps because the hardening of the wings and the development of their muscles take some time. At first only single individuals may be seen to take off in order to fly in a circle or a part of it, and to settle down again. When they fly over other individuals that are still on plants or on the ground, these also take off, probably as a reflex to the vibrations of the air (Vayssière, 1921 ; see above, p. 66). These flights, however, take place only at a certain temperature ; Sviridenko (*l.c.*) observed that the taking-off *en masse* by a swarm of the Moroccan locust occurs at 31–33·5° C., that is, at a temperature slightly higher than is necessary for the beginning of the wanderings of larval bands.

It is not clear what causes the taking off. Apparently, we must look for some internal physiological factor, dependent on temperature, which cannot be the direct cause of this behaviour.

When the whole swarm takes off, it does not settle down as quickly as do single individuals, but continues to fly for some time, usually without a definite direction, often in large circles. Such irregular flights of swarms continue every day—always in connection with the weather conditions. One swarm flying above another still on the ground may cause the latter to take off and join the first ; in this way, larger swarms are formed from small ones, exactly as happened earlier with the larval bands.

In certain gregarious species (in the Moroccan locust practically always)

such circular flights constitute the migration of swarms, but in others the flights sooner or later take the form of a direct and much more prolonged flight, in fact, an *emigration from the breeding-ground*. This emigration flight is, as a rule, taken only by large swarms, and it is remarkable for its definite direction, which usually remains practically the same during the whole flight. Unfortunately, no exact observations on a single swarm have ever been made and, therefore, the questions of the influence of the external conditions on the flight, its velocity, height from the ground, causes of stoppage, etc., have not been sufficiently studied. Organisation of observations on single migrating swarms is, therefore, highly desirable, and in this connection aeroplanes may be of great service.

From various collateral observations, it may be concluded that the emigration flight may continue, without an interruption, as long as 1–3 days and nights, and the swarm can cover during this time a very considerable distance. Flights have been in some cases observed at such a height that the whole swarm may be not visible from the ground with the naked eye. The influence of temperature on a swarm actually in flight does not seem to be so great, many cases of flight at night being known, but a sudden change in the weather, particularly rain, usually stops the flight, and the swarm settles down temporarily.

The direction of flight is to a certain extent influenced by the wind. When there is no wind, or only a slight breeze, the flight is not affected, though strong winds always carry the swarms with them. Lepiney (1928) observed that swarms of *Schistocerca* often fly towards the sun, but this seems to apply to short flights.

On the whole, however, the rôle of the external conditions in the emigration flight is of very much less importance than that of the physiological factors, which must be considered the real cause of the flight. There can be no doubt that the emigration flight is intimately connected with the process of development of the genital products. An internal stimulus for the flight during the maturation of genital products is present in other insects, such as termites and ants, in which a so-called nuptial flight precedes copulation ; this is exactly what happens in locusts. In the case of the latter this nuptial flight acquires a special regularity and length owing to the gregariousness that makes it practically impossible for a swarm in flight to stop so long as the conditions are favourable. The special physiological importance of the flight has already been discussed (see p. 51).

The emigration flight terminates either owing to very unfavourable external conditions (in which case it may be only interrupted) or, as a rule, again for internal physiological reasons, amongst which particularly important must be the exhaustion of the fat-body (by oxidation) and the reduction of the air-sacs. A swarm, which has settled after an emigration flight, reverts again to the same behaviour as before the migration, undertaking daily circular flights without any definite direction ; such flights continue until oviposition begins.

While I am firmly convinced that the emigration flight is both induced and regulated solely by physiological factors, as explained above, I feel it

necessary to give a short exposition of other theories of migration offered by other authors.

A popular view on the migrations of locusts, repeated even by some entomologists, explains them as being due to lack of food in the breeding-places. Such an idea can never occur to any one who has seen, for instance, the enormous stretches of reed-beds serving as breeding-grounds for *Locusta migratoria ;* the food resources of these grounds are literally inexhaustible, and the locusts emigrate from them when the vegetation has only been eaten over a few small patches. Moreover, the observations of Nikolsky (1911) have shown that the locusts in the emigrating swarms are practically unable to take food, at least in substantial quantity, because the digestive organs at this period are compressed by the fat-body and the air-sacs. It would be absurd to suggest in the face of this evidence that the locusts are driven by hunger. Still more absurd is the popular assumption that the " aim " of the flying swarms is to find new pastures while they leave behind them enormous supplies of their favourite food and stop again without any regard to the availability of suitable food plants. A very striking example of this kind occurred in my own experience, when in the autumn of 1912 the eastern part of the Stavropol province (in the North Caucasus) was invaded by swarms of *Locusta migratoria* which had emigrated from the permanent breeding-places of this species in the lower reaches of the river Terek. One or two of these swarms settled down in the valley of the river Kuma, which itself often serves as a breeding-place, but the majority of swarms stopped in the high open steppes adjoining the river valley. Particularly remarkable was the case of one swarm, which stopped on the slopes of the valley, actually within sight of the reed-beds, and later on, during the circular flights the swarm repeatedly flew over the valley, but was not " attracted by the sight of the green food." Ultimately, the swarm deposited its eggs on the steppe, under conditions wholly unsuitable to this species.

This observation disposes of the assumption that migration has the object of finding food supplies. At the same time, it shows equally clearly that the emigration has nothing to do with the " quest for new breeding-places," as is very often suggested. Analogous cases of the stoppage of swarms in places wholly unsuitable either for feeding or for oviposition are often recorded in the literature, and there can be only one conclusion based on them, *viz.* that it is absolutely impossible to talk of emigration having an objective ; only its causes can be considered, and these in my view lie in the physiology of the insects.

Rossikov (1899) offered another suggestion on the immediate cause of emigration, which he thinks occurs as a result of the activities of parasites (mites and flies) driving locusts out of their breeding-grounds. This theory is overthrown by the facts quoted by Rossikov himself, who states that a high infestation by the mites renders locusts incapable of flight, and that the percentage of locusts parasitised by flies is only moderately high amongst the migrating swarms, while the locusts that remain in the breeding-grounds after a migration are practically all parasitised. Detailed observations by

Nikolsky (1925) show definitely that parasites cannot be considered a direct cause of emigration, but he puts forward another theory that the emigration may be useful to the species since it enables the locusts to leave behind their parasites, which have become too numerous on the old breeding-ground, and to start breeding in a new place where they are free from parasites. This theory, in the first place, is at variance with the facts, since the most important parasites (mites and larviparous flies) are carried to the new sites by the locusts themselves ; apart from this, I find it useless to discuss theories that cannot be proved or disproved by direct observation and experiment, and that depend entirely on the assumption that everything in nature must be reasonable. In fact, however, direct observations show that the emigration of locusts from their breeding-grounds is very often a mass suicide, such as when the swarms fly straight into the open sea or have to stop and lay their eggs in the places absolutely unsuitable for breeding. Facts of this kind do not induce us to try to discover the objects of emigration and its higher significance for the preservation of species, but rather encourage us to concentrate on a detailed study of this phenomenon from the physiological standpoint.

Behaviour of Solitary Grasshoppers

Though our knowledge of the behaviour of gregarious locusts compiled on the preceding pages is far from being complete, it exceeds to a considerable extent what we know about the non-gregarious grasshoppers. This group to which the great majority of the Acrididæ belong is characterised by the absence in all stages of the tendency to form segregations.

The term " solitary " grasshoppers must not be understood in the sense that they are very rare, or occur only in very small numbers ; in a given locality there may be an outbreak of one or more solitary species and they may be present in great numbers and populate the area very densely, without, however, forming anything like swarms or bands. The main point of their behaviour is that each individual is independent of others in its movements ; the actual reason for this difference is at present quite obscure.

The reactions of grasshoppers to stimuli, on the whole, do not seem to differ greatly from what is known in locusts, except that there is no accumulation of the nervous tension, which leads to mass movements in locusts.

The daily regime of grasshoppers is also connected with the temperature, on which depend the ascent of plants, descent from them, feeding, etc. The details of their regime may differ in various species, but very little is known about the influence on grasshoppers of temperatures high enough to produce mass movements in locusts ; the facts concerning the movements of the hoppers of the solitary species have been recorded in the literature, but they have not been accompanied by observation on the temperature.

The behaviour of the adult grasshoppers also differs from that of locusts in the absence of a connection between individuals. At the same time, there is no doubt that grasshoppers can undertake migrations, sometimes even assuming the character of a mass flight. Observations of this kind are known respecting Russian and North American species, and these, during excessive

outbreaks, undertake flights resembling the emigration of a flight of locusts. A typical feature of these flights is that no dense swarms are ever formed ; the insects fly at a considerable distance from each other, though all in the same direction, determined apparently by the direction of the wind.

Further evidence in favour of voluntary flights of grasshoppers is presented by various species flying to light at night. These night flights of the solitary species seem to be connected with high temperature and low relative humidity ; thus, Rockwood (1925) observed a flight of grasshoppers of several species in Idaho on July 22, 1923, after a very hot day, at a temperature at 10 p.m. of 26·4 ° C. and a relative humidity of 25 per cent.

Another interesting fact of the same kind has been recorded by Hancock (1894) with regard to *Tettigidea lateralis*, a mass of which species settled down in the streets of Chicago during the night of September 19, 1893 ; the same phenomenon was observed two days later, and this migration of a usually very sedentary species occurred over a large area comprising the whole north-eastern corner of Illinois and the adjoining part of Indiana.

The physiology of grasshoppers is of great interest, but so far we know absolutely nothing as to the course of maturation of their genital products, the evolution of the fat-body, or the function of the air-sacs, etc. Investigations of these questions would also be of great importance for the better understanding of the analogous processes in locusts.

In any case, there are considerable grounds for suggesting that the difference between locusts and grasshoppers is not so deep seated as it might seem at first. Even the manifestations of at least partial gregariousness, under special conditions, may be observed in the typically solitary species. It may be said that gregariousness depends to a considerable extent on the density of population, and in cases of exceptionally severe outbreaks of solitary species they may behave in a way resembling locusts. Certain species are actually on the boundary line between the two groups ; here belong the Italian grasshopper (*Calliptamus italicus*) and the American *Melanoplus atlanis* which normally lead a solitary life, but during mass appearances are inclined to form larval bands and to emigrate in swarms.

Another fact in favour of the impossibility of drawing a definite line between locusts and grasshoppers is that many typical locusts are now known to possess a solitary form (phase), which differs from the gregarious phase mainly in its habits (see Chapter VII).

All these considerations lead to the conclusion that there is no deep and substantial difference between locusts and grasshoppers ; such difference as there is consists mainly in the unequal degree of reactions exhibited to stimuli and is, therefore, only quantitative. For practical purposes, however, the division of Acrididæ into solitary grasshoppers and gregarious locusts is of great advantage, since the principles of the organisation of control, and partly even its technique, must be very different in each case.

CHAPTER V

ECOLOGY AND DISTRIBUTION

Habitats

Any one who has studied Acrididæ in the field cannot have failed to notice that some species at least can be found only in places with definite natural features. Thus, the Moroccan locust cannot be expected to occur in a forest, or *Locusta migratoria* in a desert ; solitary individuals of a given species may, of course, be encountered in unusual habitats, but the abnormality of this will be obvious to any experienced observer. This phenomenon can be sometimes accounted for by the remoteness of the locality in question from the permanent habitation of the species, but in many cases this explanation does not hold, since there are many species of Acrididæ which do not go beyond the limits of very circumscribed areas and do not occur even in immediately adjoining localities with different natural features. Such places, possessing definite natural features, are called habitats of certain species, this term having, of course, not a territorial meaning, since several areas of the same habitat may be separated from each other. Examples of habitats are grass-prairie, peat-bog, reed-beds, sandy desert, etc.

The study of the interrelations of animals with the natural conditions of their respective habitats is called *ecology*, and the ecological study of the Acrididæ, though scarcely yet begun, opens up some exceptionally interesting prospects of great practical value.

Limiting Factors and Adaptability

The species of Acrididæ, when studied closely in the field, do not all prove to be equally restricted in their choice of habitats. Some of them are closely connected with one strictly defined kind of habitat and do not occur even in habitats that are very similar in their natural conditions. Some very good examples of this may be found amongst the species with desert habitats. Thus, in the shifting sand-hills of Central Asia there live several highly peculiar species of grasshoppers, *e.g. Hyalorrhipis*, *Bufonacridella*, *Diexis*, and others which are not found in any other habitat, even in the immediately adjoining sandy desert where the sand is less loose. On the stony slopes in North Africa and in other Mediterranean countries live various species of the sub-family Pamphaginæ ; these also do not occur beyond very strictly defined areas. All these are species with very narrowly defined requirements with

regard to their environment, and it is not surprising that their geographical distribution is so limited.

Other species may be found in two or three different habitats, similar in their natural conditions, as, for instance, in the grassy meadows and in the grass-steppe, or in the sandy and stony desert, etc. These species are obviously less particular as to their environment and can tolerate certain variations in its features.

There are, further, some species that live in a variety of habitats, and are, accordingly, more widely distributed.

The question arises as to what are actually the conditions that decide the choice of definite habitats by given species. From the point of view of a grasshopper, a given habitat represents only a complex of definite conditions—climatic, edaphic (soil), vegetation, etc. In respect of each of these conditions, the species has definite requirements, and, if the habitat fulfills all of them, it is a suitable one, while the absence of only one factor or its presence to an insufficient degree, make the habitat unsuitable even though all its other features are ideal for the grasshopper. This is a fundamental law of ecology—the *law of minimum*, so called because the greatest importance belongs to the factor that is present in a given environment in the minimum quantity and plays the least prominent part in its characteristics, though it decides the suitability of the habitat for the animal concerned.

Let us now discuss the ecological factors governing the distribution of grasshoppers by habitats.

Microclimate.—We have learnt in the preceding chapters that climatic conditions play a very important part in the development and in the life generally of Acrididæ, and they must be, therefore, of fundamental significance in the ecological definition of habitats. Recent ecological work has shown that for the study of the habitat conditions the ordinary meteorological observations are insufficient, since they are always made under artificial average conditions, *i.e.* such as are never experienced by animals. Meteorological stations observe temperatures, humidity, etc., in special screens at a definite height above the ground and at definite hours of the day—these all being conditions that are clearly not the same as those under which animals have to live. Further, meteorological stations observe the weather conditions for more or less wide areas, while an ecologist requires most exact data on the conditions of temperature, humidity, etc., in the very narrow and definite limits of a given habitat. Often even this may be insufficient, since we know that in order to study the conditions of movement of hoppers we must observe temperatures at different distances from the ground within the same habitat. This shows that for ecologists the study of climate of a given locality is not so important as detailed special studies of microclimates of definite habitats.

The first component of microclimate is the temperature, which must be studied by methods somewhat different from those used in meteorology. Thus, the hours of observations cannot be fixed once and for all, as they are in meteorological work, but they must always correspond to definite periods in the daily activities of the insect studied. Thus, for Acrididæ it would be necessary

to make the observations during the critical periods of the beginning and end of the movement, of feeding, etc. It is clear, also, that the number of observations must be much greater than usual ; only hourly (or even half-hourly) ones can give a sufficiently complete picture of the influence of the daily range of temperature on the activity of the insect. The exact place where the observations are made must always be chosen to represent the actual conditions of life, that is, one must always observe the actual temperature to which the insect is subjected at the moment, and this can be done only by placing a thermometer in exactly the same position with regard to the height from the ground, sunlight, etc., as the insects are themselves.

The second important ecological factor is humidity. Here, again, the usual meteorological methods are of little value in ecological work, since they do not permit estimation of the humidity in the actual immediate environment of the animals. Humidity seems to play a special important part in the selection of habitats by ACRIDIDÆ, and apparently relative humidity is more important than absolute humidity. More suitable for ecological purposes seems to be the suggestion of the leading American ecologist, Shelford, that records should be made not of the humidity of the air, but of its evaporating power. Indeed, it is less important for an ecologist to know the absolute or relative quantity of moisture in the air than to calculate its influence on the animal, and this influence consists in the degree of evaporation of water by the animal under different conditions. The evaporation, measured by the relative quantity of water lost, depends obviously not only on the humidity of the air, but also on temperature, velocity of wind, etc., so that by recording evaporation we learn the part played by several combined factors.*

A very important ecological factor for ACRIDIDÆ is presented by the vegetation. In the preceding chapter we learned that the majority of these insects are not monophagous and even not very limited in the selection of their food-plants, but we have learned also that the preferred food of very many species is Graminaceous plants. In obvious accordance with this, is the fact that ACRIDIDÆ are most numerous, both in species and individuals, in habitats with a predominance of grasses in their vegetation. For certain species a further narrowing down of habitat owing to food requirements is known ; thus *Locusta migratoria* has *Phragmites communis* as its favourite food-plant, and its typical habitats are in reed-beds.

Vegetation does not, however, influence the selection of habitat by many ACRIDIDÆ because of its food value. In fact, a study of the ecological distribution of ACRIDIDÆ shows that a very important rôle attaches to the degree of density, and partly to the height of the vegetation ; thus, a steppe with a dense, close, plant-covering harbours a fauna of ACRIDIDÆ different from that of a steppe bearing the same kinds of plants, but where they are scattered and leave bare patches between them. In these cases the vegetation cannot

* I cannot enter here into the technique of observations of ecological factors, which is, of course, the same for the ACRIDIDÆ, as in other ecological work ; those interested are referred to numerous papers by Shelford, Adams, Vestal, and other, mainly American, ecologists. For bibliography, see Pearse, A. S., *Animal Ecology*, McGraw-Hill, New York, 1926, and, especially, Chapman, R. N., *Animal Ecology with Special Reference to Insects*, Minneapolis, 1927.

influence the distribution of the insects by its food value, but it apparently acts as a microclimatic factor, owing to the shade produced influencing evaporation, etc. It must, however, here be mentioned that of great importance in the ecological distribution of the ACRIDIDÆ is the fact that they may all be roughly divided into two large groups, according to their prevailing habits. The species belonging to one group live mainly on plants, and only in exceptional cases descend to the ground; these are called phytophiles (Morse, 1904). The others, on the contrary, live normally on the ground and seldom climb plants; these are called geophiles. As examples of geophilous ACRIDIDÆ may serve, nearly all OEDIPODINÆ (*Oedipoda*, *Trimerotropis*, *Sphingonotus*, *Dissosteira*, etc.) and all TETRIGIDÆ (grouse-locusts, as they are called in America); typically phytophilous are certain species of *Melanoplus*, various species of *Chorthippus*, *Anacridium aegyptium*, etc. The two groups are not very sharply divided, since many species cannot be definitely assigned to one or the other; in the locusts we have seen that the same species may behave very differently according to external influences. Nevertheless, this quality of the ACRIDIDÆ is to a certain degree responsible for their habitat distribution, since it is impossible to expect many geophilous species in a habitat where the vegetation is dense, while habitats with many bare patches must be favourable to geophiles.

The soil is undoubtedly one of the important ecological factors for ACRIDIDÆ, mainly owing to their habit of laying their eggs in the ground and to their specific preferences in this respect (see p. 57).

ASSOCIATIONS

All animals living in a given habitat form one complex biological unit, all component parts of which are in some way connected with each other; this unit is called an *association*. It seems obvious that all animals forming a single association must possess similar ecological requirements, and that these are the actual cause of the association.

Since an association is a complete unit, it is not right to study only a part of it, as represented by the ACRIDIDÆ. This is, however, permissible, if done for practical purposes and if general ideas of ecology are not disregarded and all the members of the association directly connected with ACRIDIDÆ are taken into account. Here belong, first of all, various parasites of ACRIDIDÆ; then, the secondary parasites (hyperparasites), some of which may be connected with other insects, forming a link between the latter and ACRIDIDÆ. Insectivorous birds and other animals must be also taken into account, and their influence on the numbers of ACRIDIDÆ and other insects must be observed. In this way the part they play in the composition and life of the association may be studied, and the actual conditions of existence of the ACRIDIDÆ themselves defined.

Methods of Studying Associations.—The first problem before an ecologist is the preparation of lists of species common to certain habitats. Such lists can be complete only, if the survey of the population of the habitat has been continued throughout the whole season (a whole year in the tropics), and not

in one area, but simultaneously in several separate areas of the same habitat. It is very desirable, perhaps even necessary, to study not only the adults occurring in the habitat, but also their hoppers so far as it is practicable.

Such a simple survey is, however, insufficient, because it would give only a very crude idea of the population of the habitat, without reflecting the quantitative relations of various species in the association. It is only by means of a quantitative analysis of the population that the exact composition of the association and the relative importance of its various members may be determined.

Methods of the quantitative studies of associations have not yet been well worked out, and they cannot be the same in various cases. Thus, such striking species of ACRIDIDÆ as the OEDIPODINÆ with brightly coloured wings attract more attention than small inconspicuous species living in the grass, and one must be very careful not to be misled by the apparent predominance of the former. Differences of behaviour at different times of the day must be also taken into account.

I will now describe the actual methods of quantitative studies applied by the few ecologists who have worked on the ACRIDIDÆ.

Shull (1913) suggested a method of mass collecting and of direct count of numbers of specimens of each species ; it is clear that this method may result in a very distorted idea of the actual proportion of various species in the habitat, since less active and more conspicuous species would be collected in larger numbers than the others. It is on these grounds that Shull's method has been rejected by Vestal (1913), the author of a most valuable work on the ecology of the ACRIDIDÆ. The method used by Vestal himself was to visit the various habitats, taking one or several specimens of each species for verification, and to estimate their abundance, not from the numbers collected, but from the numbers observed per unit of area at each station, always having in mind the considerations which tend to over- or under-estimation of actual numbers, and applying to each species such methods of estimating the relative abundance as would be in accord with its habits. In this way, each species could be assigned to a definite division of the scale of abundance. The latter included the following divisions. As *dominant* was considered a species which was both very abundant and very frequent in the habitat ; *abundant*—found in the habitat, usually in considerable numbers ; *frequent*—occurring in the habitat regularly, though not always, and seldom numerous ; *occasional*—occasionally found in the habitat, not frequent or abundant ; *accidental*—occurring in a habitat unusual for the species.

The same system was adopted by Bei-Bienko (1926), but he used only four categories, instead of six, because he considered that a larger number of categories is of no advantage, as being then less clearly defined. His categories are : *abundant*—for a species, to which belong more than 50 per cent. of the population of the habitat ; *frequent*—a species, comprising 20–25 per cent. of the population ; *relatively rare*—a species, occurring in numbers, between 5–20 per cent. of the whole population ; *rare*—all species less numerous than in the last-named category.

Salfi (1924) also characterised associations by the percentage of individuals of each species, but he does not describe the actual methods of evaluation.

Kosminski (1925), apart from detailed observations on the relative frequency and abundance of species, applied a method of mass collecting in each habitat during a definite period of time. The first method gave him the possibility of forming conclusions on the distribution of species by habitats, and the second—on their relative abundance in each habitat. His categories are on a somewhat different basis and are, therefore, of special interest ; they are as follows : *leading species*—occurring only in the particular habitat ; *typical*—more numerous in the habitat under record than in any of the others ; *not typical*—more, or equally, numerous in other habitats than in the one studied ; *occasional*—not a regular member of the association. The numerical characteristics of each association were expressed by the number of specimens collected during one hour by all possible methods, average figures from a large number of counts for each habitat being used.

It is obvious that each of these methods has its advantages, but they are all based mainly on the individual valuation of the frequency of species founded on accurate and repeated observations, while the figures only give a support to the conclusions. In fact, it is hardly possible to evolve a method that would make possible an absolutely exact valuation of relative numbers of various species in the association ; I do not even think that it would be wise to adopt such a method, even if it were found, since it would tend to minimise the importance of direct observations and subjective impressions, which are of immense value in all biological work.

Grasshopper Associations.—The results attained in their study of grasshopper associations by the above-named ecologists are very interesting, especially in view of their great similarity ; this is remarkable since they all worked in widely distinct regions and quite independently.

From their results, it is clear, first of all, that grasshopper associations are richest in species and in individuals in habitats with grassy vegetation and poor in forest ones. According to Vestal, in the forest habitats studied by him, only very few species occur ; richer than the others is the association of a beech-maple forest, which includes six species, but all of them are either uncommon or accidental and occur on the margin of the forest or in the clearings ; only one species (*Melanoplus islandicus*) is restricted to this habitat and occurs in the forest itself.

In the grassland associations, the influence of humidity is well marked. Amongst the five habitats studied by Kosminski in the Bialoviez forest, the richest and most abundant grasshopper population was found in the open places with a sandy subsoil, where 16 occurred and 50–70 specimens might be collected in an hour. On the contrary, in the shore vegetation of streams and in the *Carex*-meadows only one species occurs (*Mecostethus grossus*), and not more than 10–20 specimens were collected in an hour. Bei-Bienko also found that in the Altai the grasshopper associations are richest in xerophytic habitats.

If the habitats of a given locality are placed in series according to the degree of humidity, at both ends there will be associations with the fewest species, but these will include many restricted to these particular habitats. This shows that an extremely dry environment is unfavourable to the majority of species, except for those specially adapted to it.

Amongst the species that occur in several habitats, a different degree of "ecological plasticity" (Bei-Bienko) may be observed: some of them occur both in xerophytic and mesophytic habitats, while the majority are more restricted in their distribution, showing in this way a varying adaptability to fluctuations in the conditions of environment. Quantitative studies on the species possessing great plasticity show that even they, though occurring in many habitats, are always more numerous in one or two of them, *i.e.* they also exhibit a definite preference for certain ecological conditions. This preference is very strictly specific; so far no two grasshopper species have been found to have identical habitat preferences, and no two habitats possess an identical grasshopper population.

External Evidence of Environmental Conditions.—A study of the external characters of the species living in habitats similar in their conditions shows very clearly that the environmental factors are of great importance in this respect. For instance, the species living in various countries in grassland habitats (steppes, savannas, prairies) are remarkable for their generally slender build, often ensiform antennæ, elongated head, relatively feeble jumping legs, and pale-green, straw-yellow, or brownish coloration, often with longitudinal stripes; these characters repeat themselves in species entirely unrelated to each other. Similarly, the inhabitants of the deserts of the whole world may be recognised by a more or less depressed body with a very rough surface, short, vertical head, and a coloration closely corresponding to the colour of the ground. In this connection it is particularly interesting to quote the example of the Australian fauna, where the bulk of the species belongs to one subfamily, the Catantopinæ, the members of which have developed into a number of genera absolutely parallel both to the phytophilous and geophilus genera of other countries, though not at all related to them. This implies that the similar ecological conditions of existence may produce very similar effects in different species.

The influence of environmental conditions is particularly clearly shown by the coloration, which very often closely corresponds to the general colour of the surroundings. It is important to observe that the general colour of adult Acrididæ varies to a considerable extent within the same species, so that in the phytophilous species colour forms may be found that correspond with all possible shades of green, drying, and dry vegetation; in the geophilous species there is usually a great variety of forms, apparently harmonising in their colour with different kinds of soil. All such cases of homochromy are usually explained by the adaptation resulting from the natural selection, which eliminates all colour forms insufficiently protected from enemies by their coloration. Detailed observations, however, do not tend to confirm this purely theoretical deduction. Rabaud (1923) has proved very conclusively

that in the two species of *Oedipoda*, in which a series of colour forms of various shades similar to the ground may be observed, there is no connection between the shade of a particular colour form and the colour of the actual ground where it was taken. This author, therefore, is inclined to accept the suggestion made by Vosseler (1902), who reached it after a study of the Orthoptera of the Sahara, namely, that the coloration of each individual is a result of the action of coloured rays on the freshly moulted insects, which, as we know, only acquire their coloration gradually. In this way, each individual would acquire a colour more or less corresponding to the colour of its immediate surroundings just after the moult, but later on it can, and often does, move on to a differently coloured ground, where its "protective" coloration makes it conspicuous. The weak spot of this hypothesis is the absolute lack of knowledge of the pigments involved and of their development in the presence of light rays, but in any case it provides definite problems that can be studied by exact methods, while the usual theory of the protective function of coloration must be taken on faith. Eisentraut recently attempted (1927) to obtain experimental evidence on the problem, but with indefinite results.

In the morphological characters of Acrididæ we can also find numerous examples of the direct connection between the structure of the insect and the environmental conditions. For example, all phytophilous species have strongly developed pulvilli between the tarsal claws, which help in climbing, while in the geophiles, the pulvilli are either very small or even absent. The shape of the ovipositor of the females depends on the physical properties of soil, where the eggs are usually laid, while in species that do not lay their eggs in the soil, the ovipositor is of abnormal form ; thus, in *Chrysochraon dispar* the ovipositor is absolutely unsuitable for digging, but well adapted for splitting dry stems, into which the eggs of this species are usually laid (Shapinsky, 1923*a* ; Ramme, 1927).

Classification of Associations.—The only attempt to give a classification of grasshopper associations was made by Morse (1904). This author attributes special significance to the grouping of Acrididæ into geophiles and phytophiles, and he accordingly divides all associations into these two parallel groups. This point of view cannot be accepted, since not only is it impossible to draw a sharp dividing line between phytophiles and geophiles, but it is obvious that all species living in a given habitat form one association, whether they live on plants or on the ground.

In Morse's classification a further subdivision of associations is presented as follows :

Geophilous division.
- Campestrian group.
  - Xerophile societies.
    - Saxicolous species.
    - Arenicolous species.
    - Humicolous species.

Phytophilous division.
- Campestrian group.
  - Xerophile societies.
  - Hygrophile societies.

Hygrophile societies.
Humicolous species.
Paludicolous species.
Limicolous species.
Sylvan group.

Sylvan group.
Thamnophile societies.
Dendrophile societies.

The main fault of this classification is that it has no unity of principle, since the associations are arranged into groups by one character, and the further subdivision is based on another.

More acceptable and, perhaps, the only possible one is the scheme offered by Vestal, who does not set himself the task of outlining a general classification of associations, but merely presents a natural system of the associations of one area, while he regards associations from the point of view of their origin from each other as being parallel to the changes in the environment, as we shall see later on.

Dynamics of Associations

When two habitats adjoin each other (as for instance a meadow and a swamp, or a steppe and a forest), there is between them a border-zone in which the elements of both associations come into a close contact, without being specially adapted to each other, as the members of a single association are. The significance of this zone is particularly great because of the natural tendency of each association to extend its limits, which results in acute competition in the border-zone. If, at the same time, the general conditions of the whole region undergo a gradual change into a direction favourable to the one of the two associations, the latter will steadily extend its area at the expense of the other.

Such a competition between associations is continually going on everywhere in connection with the geological processes of denudation, climatic fluctuations, etc. The main moving force of these successions of associations is their tendency to extend, while all other factors serve only to facilitate the victory of certain associations over others. The whole process, in most cases, is too slow to be observed directly, but it is possible to study it by the indirect method, which consists in observations on the interrelation of associations in a given natural area, where the tendency of certain associations to extend at the cost of others cannot escape the attention of the observer.

The process of succession of habitats has a special importance for the Acrididæ, which are very sensitive to slight alterations in the environmental conditions, and Vestal, in his admirable work on the grasshopper associations of the Douglas Lake region, has given a most interesting outline of changes in the grasshopper population of one area. The succession of habitats in the area is caused (or, more correctly, directed) by the gradual drying up of some lakes, the shores and bottoms of which are occupied by land vegetation; various species of grasshoppers appear at different stages of the process, as will be seen from the following table, in which five subsequent habitats and their grasshopper species are shown :

	Bare sand.	Beach grass.	Bracken-blueberry.	Aspens.	Beech-maple.
Dissosteira carolina	Freq.	Freq.	Occas.	—	—
Spharagemon bolli	Freq.	Occas.	Occas.	—	—
Circotettix verruculatus	Freq.	Occas.	Occas.	—	—
Arphia pseudonietana	Freq.	Infreq.	Infreq.	—	—
Hippiscus tuberculatus	Freq.	Infreq.	Infreq.	—	—
Camnula pellucida	Freq.	Freq.	Freq.	—	—
Melanoplus angustipennis	Occas.	Freq.	Domin.	—	—
Melanoplus luridus	—	—	Occas.	—	—
Scirtetica marmorata	—	—	Infreq.	—	—
Melanoplus fasciatus	—	—	Infreq.	Freq.	—
Chloealtis conspersa	—	—	?	Infreq.	—
Podisma variegata	—	—	—	—	?
Melanoplus islandicus	—	—	—	—	Freq.
Melanoplus atlanis	Freq.	Abund.	Freq.	?	Infreq.

It will be seen from this table that the initial stage of the evolution is bare sandy beach, inhabited by eight species of grasshoppers, most of them (five) being typical geophiles. Next the sand becomes covered with grasses, and this causes the geophiles to become less numerous, while in the next stage, when the vegetation is denser and consists mainly of *Vaccinium* and bracken (*Pteris*) with various grasses, but without trees, the number of grasshoppers is the largest and the geophiles give way to phytophiles. After that, the aspen forest begins to grow, and this immediately reduces the grasshopper population to two species only, both phytophilous ; in the still denser beech-maple forest which replaces that of aspens, there are also only two phytophilous species.

Analogous schemes of succession of grasshopper associations may be drawn for all actual cases, and this would be of the greatest practical value in the areas where certain injurious species are normally breeding, but so far no work has been done in this direction.

Equally, if not more, important for the economic entomologist are observations on the succession of associations following changes in the environment brought about by the activity of man, such as cultivation. When the virgin steppe is first ploughed, this immediately influences the grasshopper population; for example, the Moroccan locust ceases to breed in the areas that are under cultivation ; the same happens to many other species, but there are others that find the new conditions acceptable and even favourable ; as a result, the whole population is entirely changed. Facts of a similar kind are well known, but no serious work has been ever done to estimate accurately the influence of various methods of agriculture on the grasshopper population.

Cultivation of the soil is not the only thing that introduces changes affecting grasshoppers ; even the grazing of cattle may have a very profound effect. Two Canadian entomologists, Treherne and Buckell (1924), who have studied the grasshopper problem in British Columbia, found that this is directly dependent on the amount of grazing. The normal type of prairie there is covered by short grass, and the normal population consists of a small number of species of grasshoppers occurring in moderate numbers. An immoderate grazing results in the destruction of grasses, which are replaced by various weeds, scattered widely

over practically bare ground, and these conditions prove to be very favourable to several, mainly geophilous, species of grasshopper, which breed in large numbers and complete the extermination of the grasses. Experiments in fencing in areas of prairie in order to keep the cattle out resulted in a few weeks in the reappearance of the normal vegetation and of the corresponding grasshopper association, both being in a perfect balance.

A very similar case may be observed in the Russian steppe areas where there are common grazing grounds near the villages ; these are usually overgrazed and become veritable breeding-places for various grasshoppers, which, from them, invade the adjoining cultivated lands, on which they cannot breed.

When studying the dynamics of the associations, it must be borne in mind that some species of Acrididæ are inclined to move temporarily from one habitat into another. In the case of locusts this occurs without any regularity, owing to their wanderings, and this often leads to most serious mistakes in the definition of their normal habitat ; as an example may be taken the Moroccan locust, which normally inhabits dry stony hills, though in the years of its mass appearance, its migrating swarms lay their eggs under very different conditions on the grass steppes ; these until recently were incorrectly considered the normal habitat of the species, because all observations on it were made during these exceptional years.

Among the non-gregarious grasshoppers the fact of a migration connected with the seasons is known to occur. Thus in the Russian steppes at the end of summer, when the grasses in the open steppe are scorched by sun, the bulk of the grasshopper population shifts into hollows where the vegetation remains green longer. Bei-Bienko (1928) observed that various Siberian grasshoppers migrate more or less regularly from one habitat to another as the hoppers grow and the adults appear.

In *Locusta migratoria* habitat changes with development ; the hoppers and adults live amongst the reeds, but for oviposition the latter select more open and dry places on the borders of the reed-beds, very seldom depositing their eggs in the latter. It is not impossible that a similar difference between the habitat and the places selected for egg-laying exists in other species, and this makes it impossible to accept the view of American ecologists who consider the habitat in which it lays its eggs to be the normal one for the species ; this view does not recognise the changes that occur in the habitat of a species during its individual life.

Geographical Distribution

Areas of Distribution.—The region populated by a species, or the area of its geographical distribution, may be more or less large, for a variety of reasons. As a rule, the more widely distributed species are those with the greatest ecological plasticity that are thus able to find suitable conditions of existence more easily. In any case, the ecological characteristics of a species are responsible to a very great degree for its distribution.

The area of distribution may be either continuous, if the species populates a large uninterrupted region, or discontinuous. An example of the latter

is the Siberian grasshopper (*Gomphocerus sibiricus*), which inhabits the whole of Siberia and Eastern and Northern Europe, but disappears further to the South and to the West, only to be found again in the mountains of the Caucasus, Alps, and Pyrenees. Cases like this cannot be explained on ecological grounds, and past geological history must be taken into account (see below).

In the case of the injurious species, it is necessary to distinguish between their area of general distribution and the area where they occur as a pest. That these areas may be, and often are, different, may again be seen in the Siberian grasshopper, which is very injurious in Siberia, but harmless (apart from exceptional cases) in the Caucasus and in Europe, though it occurs there in considerable numbers. The reason for this must lie in some slight ecological differences between the parts of the area of general distribution, only that part with the optimum conditions for the species being able to support it in sufficiently large numbers for it to become injurious.

In the case of locusts, there must be further recognised the areas of permanent habitation, or *breeding-grounds*, where the species lives always and whence it undertakes migrations in the years of mass development ; at such times it can temporarily settle in areas that are not normally inhabited by it. Thus the following three categories must be distinguished in the case of the gregarious locusts : (1) permanent breeding-grounds, (2) temporary breeding-grounds, and (3) areas of permanent habitation of the solitary form, which can transform into the swarming form only in the two preceding categories.

Factors of Distribution.—It is clear from the above, that the main cause of the extent of the area of a given species is its ecological character, but this is not the only factor. Indeed, the distribution of the Siberian grasshopper quoted above can only be satisfactorily explained, if the past geological history of the country is taken into account. In this particular case, the species was originally evolved in Asia and could have penetrated into Western Europe only during and immediately after the Glacial period, when steppes of the Siberian type stretched across the whole of Europe ; a further change of climate after the Glacial period resulted in a complete change of the ecological conditions, and the Siberian grasshopper has survived in Western Europe only in isolated places where the conditions are still more or less similar to the original ones.

In order to understand the present area of distribution and of the injurious activities of a species of grasshopper, it is necessary, therefore, not only to know its ecology intimately but also to appreciate the ecological history of the country where it occurs. It is also imperative to study the ecology of an injurious species not only in the area where it is actually a pest, but in the whole area of its geographical distribution, since only then will it be possible to understand the reasons for it becoming a pest in a certain part of its area, and this may lead to valuable suggestions with regard to control.

CHAPTER VI

NATURAL ENEMIES

Amongst the natural enemies of Acrididæ there are many that may be considered more or less constant factors in their biology, while others play only an occasional rôle in their life. In the following chapter I aim at giving a full outline of the life-history and interrelations with the Acrididæ of only those belonging to the first group ; and as regards occasional enemies, the information given must not be regarded as exhaustive.

Parasites and Enemies of Eggs

The eggs of Acrididæ are liable to attack from a fairly numerous group of insects closely connected in all their development with them ; next in importance are mites, then fungous and bacterial diseases, while the last place is occupied by more or less accidental enemies of the eggs, such as birds, the larvæ of some carnivorous insects, etc.

Amongst the insects, those dependent for their development on the eggs of Acrididæ belong to three main kinds : beetles of three different groups, flies and parasitic Hymenoptera.

Blister Beetles of the Genus Mylabris.—The beetles of this very large genus, characterised by their yellow, or orange, elytra with black bands or spots (Fig. 47, B), are very common in most countries of the Old World, occurring on flowers, particularly Umbelliferæ.

The life-history of those species that have been studied, and these are very few, may be outlined as follows (Portchinsky, 1914 ; Roepke, 1917).

A female, in laying its eggs, digs with its front legs a little hollow in the ground, somewhat longer than the insect itself. It is worthy of special note that this is usually done in very hard ground, *e.g.* on the sides of roads and not in soft ground, where the operation would be easier because the front legs are not in any way adapted for digging. There are no data as to whether the females are guided in the selection of places for oviposition by the presence of the eggs of Acrididæ ; as a matter of fact, there are not even any exact observations showing that the places selected are those ecologically suitable for Acrididæ, though collateral evidence in favour of this may be seen in the fact that the species of *Mylabris* lay their eggs in the hard soils that are also preferred by many species of grasshoppers.

When the hole is made, the female enters it with the hind end of the abdomen first and lays a group of 24–60 eggs ; it then comes out and fills up

the hole with earth, which it conveys in bits with its mandibles and front legs, finally trampling it down with its hind legs.

The eggs are oval in shape and rather large in relation to the size of the beetles, being 2–2½ mm. long (in the large Javanese *M. pustulata* more than 3 mm.). The development of the embryo in the egg occupies 14–22 days, after which period a very curiously shaped larva hatches (Fig. 47, Tr).

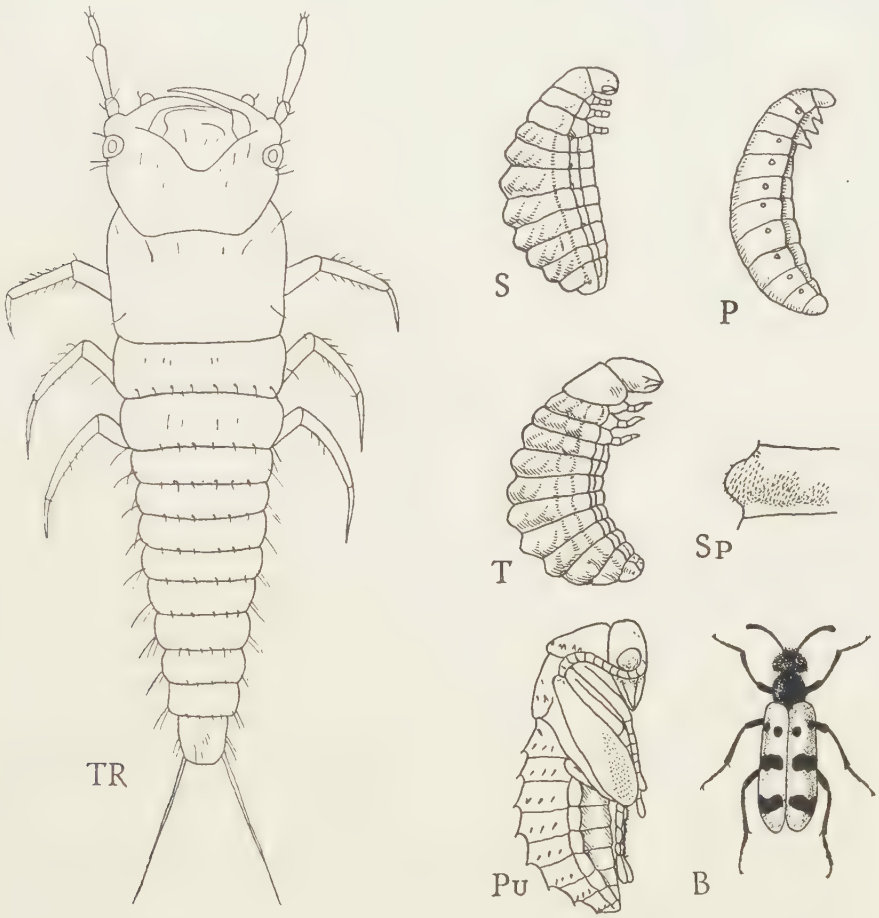

Fig. 47.—Metamorphosis of a *Mylabris*.—Tr, triungulin (of *M. crocata*, after Pukhova).—S, second larva.—P, pseudopupa.—T, third larva.—Sp, a segment of the third larva to show the spinules.—Pu, pupa.—B, adult beetle (after Portchinsky).

This first larva of *Mylabris* is called a *triungulin*. Its body is elongated, narrowed behind, and consists of thirteen segments including the head which bears strong mandibles, relatively large ocelli, a pair of short four-jointed antennæ and a pair of small palpi; the legs are long and slender, and each is armed with three claws. The whole body is covered with sparse hairs, the number and arrangement of which is typical for each species, as also are the details of the structure of the antennæ, palpi, and the shape of the segments of the body. At the hind end of the abdomen, there is a pair

of long bristles. The size of triungulins varies, according to the species. from 3 to 5 mm.

The newly emerged triungulin runs rapidly on the surface of the ground, entering crevices, etc., until it finds the egg-pod of a grasshopper, which it promptly enters. It is still unknown how triungulins find the egg-pods that lie deep in the ground or how they enter egg-pods with a solid hard lid ; indeed, there are hardly any observations on the behaviour of triungulins at all.

As soon as a triungulin enters an egg-pod, it undergoes a transformation ; it is, however, unknown whether a triungulin needs to feed, or whether it moults immediately on entering the pod. The next stage of development, the so-called *second larva* (Fig. 47, S), is entirely unlike a triungulin, both in its behaviour, being almost unable to move, and in its general appearance. The body of the second larva is thick and somewhat curved ; the head has black eyes, but no antennæ ; the mandibles are fairly well developed ; the legs each bear one black claw. The dorsal segments of the body are strongly convex longitudinally, and are separated from each other by depressions ; each segment is also provided with longitudinal furrows on the convex surface. With the growth that results from feeding on the eggs in the pod, the larva becomes thicker, the convexities on its body become less prominent, and the legs become shorter, almost like mere tubercles, so that the larva can hardly move. The full development of this larva apparently occupies a few days, but there are no exact data.

After reaching full size, the second larva moults and transforms into the next, motionless stage—*coarctate larva*, or *pseudopupa* (Fig. 47, P). This transformation occurs, in the case of species that parasitise egg-pods with hard walls, inside the pod, but from pods with thin walls the larva may crawl out into the surrounding soil. The pseudopupa is similar to the full-grown second larva in general shape, but the segments are less distinct ; the head is small, well separated from the body, and bears rudimentary mouth-parts ; the legs are very short and tubercle-like. The winter in temperate regions is passed in this stage, so that it is the one best known to entomologists, who meet with it when taking samples of egg-pods in the breeding-grounds of grasshoppers.

No further transformation normally occurs until next spring, though pseudopupæ that are brought into a warm laboratory moult in winter. The next stage is the *third larva* (Fig. 47, T), which is very clumsy and has short legs without claws ; its body is inflated in the middle, tapering to both ends, but more strongly anteriorly ; the head is small, without antennæ, but with mandibles ; the segments of the body are convex and with tubercles which bear minute spines (Fig. 47, Sp). The third larva can move, though very awkwardly, and it has not been proved by direct observations whether it can find an egg-pod, if the pseudopupa was not in one.

After devouring some eggs, the third larva transforms into the true *pupa* (Fig. 47, Pu), in which all parts of the future adult insect can be seen. The beetle emerges after a short pupal period so that the whole development occupies a full year in the temperate regions. In exceptional cases, however,

development may take still longer; Bezrukov (1922) records a case where pseudopupæ of *Mylabris quatuordecimpunctata* hibernated twice.

The economic importance of *Mylabris* spp., as regulators of grasshopper numbers, is very great, and there are many records of a practically complete infestation of egg-pods by their larvæ. At the same time, it must not be forgotten that the above outline of the bionomics of these parasites is very incomplete and is based on observations on very few species of these beetles, which may differ considerably both in their bionomics and in their economic rôle.

Before proceeding to give a list of the species of *Mylabris* recorded as parasites of various species of ACRIDIDÆ, I must point out that this list is based entirely on records in the literature. These it has not been possible to verify, and the responsibility for them rests with the authors of the papers quoted; special caution is necessary in dealing with the records given by Portchinsky (1914), because he appears to have been misled in some cases by insufficiently reliable observers. The species are given in alphabetical order.

List of species of Mylabris, parasitising the egg-pods

M. calida, Pall.—*Locusta migratoria*, *Calliptamus italicus*, *Arcyptera microptera*; Russia (Portchinsky, 1914; Modestov, 1921).

M. cincta, Ol.—*Dociostaurus maroccanus*; Turkestan (Portchinsky, 1914).

M. crocata, Pall.—*Arcyptera microptera*; Russia (Portchinsky, 1914; Modestov, 1921; Pukhova, 1923, description and figure of triungulin). (A record by Portchinsky that this species has been bred from the egg-pods of the Moroccan locust in Siberia is based on a mistake, since this locust does not occur there.)

M. decempunctata, F.—*C. italicus*, *A. microptera*, *Dociostaurus brevicollis*; Russia (Portchinsky, 1914; Modestov, 1921).

M. floralis, Pall.—*A. microptera*, *A. fusca*, *Podisma pedestris*, *D. maroccanus*; Russia (Portchinsky, 1914, development, figures of larval stages; Ingenitsky, 1898; Modestov, 1921); *D. maroccanus*, Montenegro (Baranov, 1924).

M. frolowi, Germ.—*L. migratoria*, *D. maroccanus*; Russia (Portchinsky, 1914, figure of triungulin).

M. fusca, Ol.—*D. maroccanus*; Russia (Portchinsky, 1914).

M. geminata, F.—*A. microptera*; Russia (Portchinsky, 1914).

M. geminata subsp. *sibirica*, F. W.—*A. microptera*, *Chorthippus scalaris*, *Stenobothrus lineatus*; Russia (Portchinsky, 1914; Pukhova, 1923, description of the triungulin).

M. ledereri, Mars.—*L. migratoria*; Russia (Portchinsky, 1914).

M. magnoguttata, Heyd.—*D. maroccanus*; Russia (Portchinsky, 1914).

M. ocellata, Pall.—*Calliptamus italicus*; Russia (Portchinsky, 1914).

M. pustulata, Thbg.—*Valanga nigricornis*, Java (Roepke, 1917, development, figures); *Hieroglyphus banian*, S. India (Coleman and Kuhni Kannan, 1911, somewhat indefinite record).

M. quadripustulata, L.—*L. migratoria*, *C. italicus*, *D. maroccanus*, *Podisma pedestris* (Portchinsky, 1914; Modestov, 1921).

M. quatuordecimpunctata, Pall.—*A. microptera*, *A. fusca*, *C. italicus*, *Dociostaurus kraussi ;* Russia (Ingenitsky, 1898 ; Portchinsky, 1914, figure of triungulin ; Moritz, 1915 ; Modestov, 1921 ; Bezrukov, 1922 ; Pukhova, 1923 ; Vorontsovsky, 1926).

M. schreibersi, Rch.—*D. maroccanus ;* Algeria (Künckel, development, figures).

M. sexdecimpunctata, Gebl.—*Dociostaurus kraussi ;* Russia (Portchinsky, 1914).

M. tekkensis, Heyd.—*D. maroccanus ;* Russia (Portchinsky, 1914).

M. tripunctata (?)—*L. migratoria ;* Russia (Rossikov, 1894 ; the name of this parasite must be incorrect, since *M. tripunctata*, Thnbg., is a South African species).

M. variabilis, Pall.—*A. microptera ;* Russia (Portchinsky, 1914) ; *D. maroccanus ;* Montenegro (Baranov, 1924 ; doubtful record).

M. variabilis var. *lacera*, Küst.—*D. maroccanus ;* Sicily (Stefani Perez, 1913 ; development, figures).

It will be seen from this list that a more or less complete description of the development exists only in respect of four species of *Mylabris*, and in only three more are the triungulins known, while all the others are simply recorded as bred from the egg-pods ; even this requires checking in some cases.

The beetles of this genus sometimes themselves become serious pests of various plants, particularly vegetables ; this usually happens in the years following a mass development of local species of ACRIDIDÆ and is a direct result of it.

Blister Beetles of the Genera Epicauta and Macrobasis.—These beetles are related to *Mylabris*, but are much more slenderly built and are of a blackish or brown colour, often with pale longitudinal bands on the elytra (Fig. 48, G). They also occur on flowers, but are more agile than species of *Mylabris*.

The development of these beetles is similar to that of *Mylabris* (see Portchinsky, 1914 ; Beauregard, 1890 ; Riley, 1878 ; Roepke, 1917). The female makes a hole for oviposition, but is not particularly careful in filling it up and levelling the place afterwards (Pukhova, 1923). The number of eggs in one batch is said by Pukhova to be 50 for *E. megalocephala*, but Riley records 130 as the average for the North American species, and states that a female lays several times. The triungulins that hatch from the eggs are similar to those of *Mylabris*, but they are known only in very few species ; the triungulins of *E. megalocephala* (Fig. 48, A) and *E. ruficeps* attract attention by their very large heads narrowed behind like a neck.

After entering an egg-pod, the triungulin transforms into the *second larva* (Fig. 48, B), which, after devouring some eggs, become much thicker and more bent (Fig. 48, C) ; this difference has led some authors to call this larva at the end of its growth the third larva, but this is obviously incorrect, since there is no moult, and the practice introduces a confusion ; an analogous change in the second larva occurs in *Mylabris* also, but it is there less marked. The second larva usually leaves the egg-pod and transforms in the soil into the *pseudopupa* (Fig. 48, D) ; the latter is similar to that of *Mylabris* and has

very hard outer coverings. The pseudopupa hibernates and transforms in the next spring into the *third larva* (the fourth, according to some authors), which differs from the second larva by its somewhat smaller size and less bent body of a pure white colour (Fig. 48, E); the legs are very little developed and are short, with one claw each. According to Portchinsky, the third larva changes its place in the soil and then moults into the *pupa* (Fig. 48, F), from which an adult insect emerges after 5 to 6 days. Riley also observed that the third larva moves about in the soil, but it is unknown whether it takes any food; in his experiments transformation into the pupa occurred without feeding.

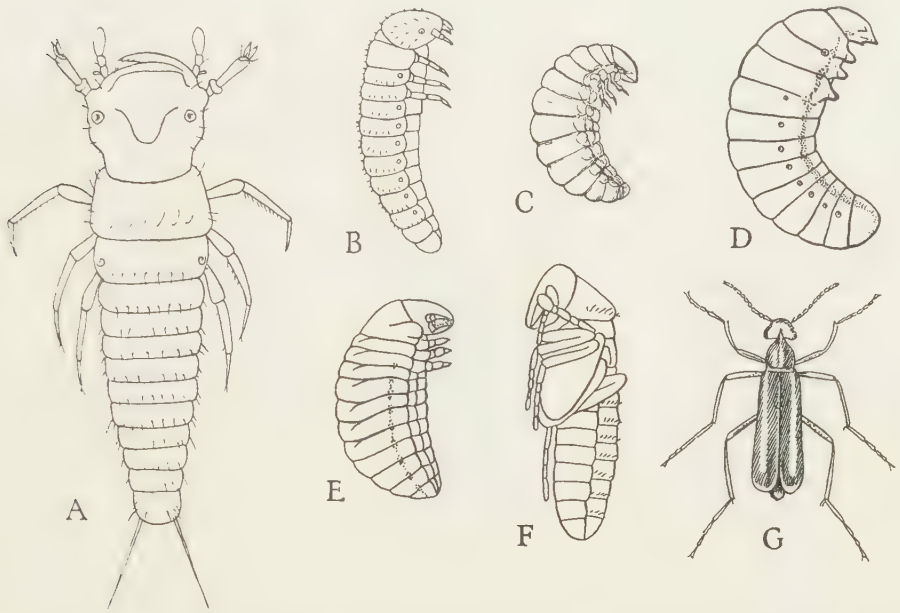

FIG. 48.—Metamorphosis of *Epicauta*.—A, triungulin (of *E. megalocephala*, after Pukhova).—B, second larva, before feeding.—C, ditto, after feeding.—D, pseudopupa.—E, third larva.—F, pupa.—G, adult beetle of *E. erythrocephala* (after Portchinsky).

List of species of Epicauta and Macrobasis feeding on Acridid eggs

E. adspersa, Kl.—*Dichroplus vittatus*, Argentina (Brèthes, 1917).

E. atomaria, Germ.—*Dichroplus vittatus*, Argentina (Brèthes, 1917).

E. erythrocephala, Pall.—*Locusta migratoria*, *Calliptamus italicus*; Russia (Portchinsky, 1914, development, figures of the third and second larva, pseudopupa and pupa; the record of this author that this species occurs in the pods of *Gomphocerus sibiricus* is doubtful).

E. megalocephala, Gebl.—*Gomphocerus sibiricus*, *Chorthippus scalaris*; Siberia (Ingenitsky, 1898; Portchinsky, 1914; Pukhova, 1923, description and figure of triungulin).

E. ruficeps, Ill.—*Valanga nigricornis*, Java (Roepke, 1917, development, figures).

E. sibirica, Pall.—*Arcyptera fusca*, *A. microptera*, *Gomphocerus sibiricus* (Ingenitsky, 1898; Portchinsky, 1914).

E. rufidorsum, Goeze (*verticalis*, Ill.).—*Dociostaurus maroccanus*, Montenegro (an indefinite record by Baranov, 1914; Bauregard, 1890, described a triungulin which he fed in captivity on the eggs of *Oedipoda coerulescens*).

E. vittata, F.—*Melanoplus differentialis*, N. America (U.S. Ent. Commission, 1877).

Macrobasis cinerea, F. (*unicolor*, Kby.).—*Melanoplus differentialis*, N. America (Morgan, 1901).

This list shows that our knowledge of this group, as parasites of ACRIDIDÆ, is very meagre, the triungulin stage being known for one species only, while the information on the habits and parasitic activities of each species is of a most fragmentary nature. This makes an estimate of the economic importance of these undoubtedly serious enemies of ACRIDIDÆ practically impossible.

Beetles of the Genus Trichodes.—These beetles resemble in the general scheme of their coloration members of the genus *Mylabris*, their elytra being metallic green with red spots or bands, but harder in texture than in *Mylabris* (Fig. 49).

FIG. 49.—A, larva of *Trichodes amnios*, F.—B, beetle, and C, larva of *Trichodes umbellatarum*, Ol. (after Künckel).

Several species of this genus are known to be enemies of the egg pods of the Moroccan locust (*Dociostaurus maroccanus*):

T. amnios, F.—Algeria (Künckel); Portugal (Seabra, 1901); Sicily (ab. *flavicornis*, Germ., Stefani Perez, 1913); Anatolia (La Baume, 1918).

T. laminatus, Chevr.—Mesopotamia (Jackson, 1926).

T. umbellatarum, Ol.—Algeria (Künckel).

The biological data on species of *Trichodes* are very incomplete. The beetles have been observed in Mesopotamia in large numbers amongst ovipositing swarms of locusts. The eggs, according to Seabra, are laid singly in each egg-pod, but this statement appears to be based on the presence of only one larva in each pod, and not on direct observations. The development of the larvæ occurs without the complicated transformations described above for *Mylabris* and *Epicauta*, *i.e.* the stages of larva are similar to each other, and there is no intermediate resting pseudo-pupal stage. The larvæ (Fig. 49, A, C) are agile, pale-pink in colour, the body being somewhat depressed and widest behind the middle; the head small and without eyes; the posterior end of

the body with two short chitinous spines. The pupa is also pinkish in colour ; pupation apparently takes place in the egg-pod.

Bombyliid Flies.—Amongst the Dipterous family BOMBYLIIDÆ there are many species, parasitism by which in the larval stage in the egg-pods of ACRIDIDÆ is fully established, and their economic importance is considerable. In spite of this, we know very little even with regard to the main points in the bionomics of these flies.

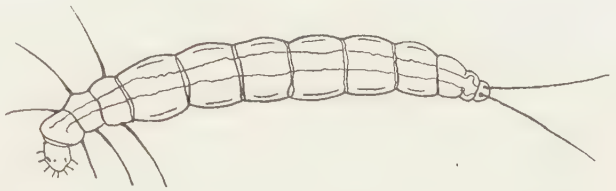

FIG. 50.—First larva of a Bombyliid fly (after Portchinsky).

The adults (Fig. 51, A) occur fairly commonly on flowers of various plants and are remarkable for their habit of not settling on the flower, but of sucking the nectar with their long proboscis while hovering over it.

Oviposition in the species that parasitise ACRIDIDÆ has never been observed, but in other species the female simply flies very low over the ground and from time to time nearly touches it, each time dropping an egg. The first

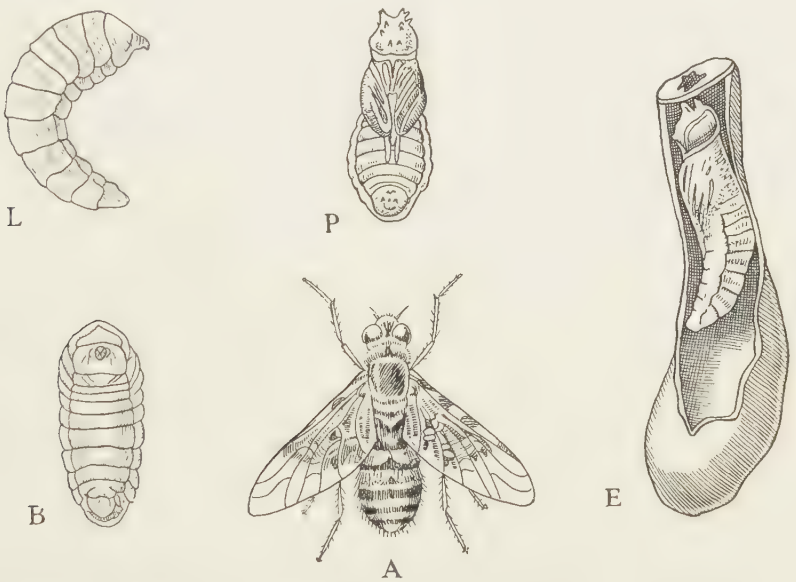

FIG. 51.—Metamorphosis of *Thyridanthrax fenestratus*, Fall.—L, larva.—B, ditto, seen from below —P, pupa.—E, ditto, emerging from the egg-pod.—A, adult (after Künckel).

larva emerging from the egg is also known only in the species that are not connected with ACRIDIDÆ ; it is very small (Fig. 50), and provided with three pairs of bristles instead of legs, by means of which it can move very rapidly and find its food ; this larva clearly corresponds to the triungulins of *Mylabris* and *Epicauta*.

Finding the egg-pod does not seem always to be an easy task, since in

Systoechus autumnalis many of the larvæ are usually unable to do so in autumn when they hatch, but have to hibernate in the soil and resume their quest next spring (Portchinsky, 1895).

After entering the pod, the larva moults and reaches (perhaps after two moults) a stage that is well known, because it is commonly found in the pods when samples are taken from breeding-places in autumn and spring. The larva in this stage is a yellowish, clumsy creature, without any trace of legs, eyes, or anntenæ, but with black-pointed chitinous mandibles (Fig. 51, L, B). The absence of legs enables a Bombyliid larva to be distinguished from that of *Mylabris* or *Epicauta*.

As stated above, the larva hibernates in the pod, continuing next spring to feed on the eggs and only pupating in late spring. The pupa has a very peculiar appearance owing to the presence of several pairs of strong spines on its head and of transverse rows of small spinules and bristles on the abdominal segments (Fig. 51, P). The significance of these structures becomes clear when the adult fly starts emerging from the pupa ; the pupa forces its way to the surface of the ground with its head, while the abdominal spines ensure a firm support (Fig. 51, E). When the pupa reaches the surface and even protrudes a little beyond it, its skin bursts on the back and the adult fly emerges ; the latter is such a fragile creature that it would be utterly impossible for it to overcome even the feeblest obstacles.

The data at our disposal enable us to state that the larvæ of Bombyliids probably do not destroy more than the contents of one egg-pod each. Moreover, my own observations show that they often are not fully successful even in that ; I have several times seen a larva that had eaten only a few eggs in a pod, when the remainder were already hatching. This proves that the usual estimation of percentage of destruction of eggs by calculating the percentage of the egg-pods containing larvæ may give a very incorrect idea of the actual state of things. Apart from this, there are reasons for supposing that some Bombyliids do not live in the larval stage exclusively on Acridid eggs, but possibly feed on roots and other vegetable matter as well (La Baume, 1918).

List of Bombyliids, parasitising the egg-pods *

Thyridanthrax fenestratus, Fall.—*Dociostaurus maroccanus*, *Ocnerodes* ; Algeria (Künckel, development, figures) ; *Arcyptera microptera*, Siberia (Bezrukov, 1922).

T. perspicillaris, Loew.—*A. microptera*, Siberia (Troitsky, 1914).

Spongostylum (*Argyramoeba*) *isis*, Meig.—*D. maroccanus*, Syria (La Baume, 1918).

Callistoma fascipenne, Macq.—*D. maroccanus*, Anatolia (Calvert, 1881, figures ; La Baume, 1918, bionomics, figures).

C. desertorum, Loew.—Probably *D. maroccanus*, Turkestan (Portchinsky, 1894).

Cytherea (*Mulio*) *obscura*, Meig.—*D. maroccanus*, Crimea (Stepanov, 1881, figures) ; Sicily (Stefani Perez, 1913 ; development, figures).

* Generic nomenclature after Bezzi, *Bombyliidae of the Ethiopian Region*, 1924.

Anastoechus nitidulus, F.—*D. maroccanus*, Transcaucasia (Stepanov, 1882, figures; Schimkewitch, 1884); Portugal (Seabra, 1901); *L. migratoria*, Astrachan (Sacharov, 1913); *Gomphocerus sibiricus* and *Chorthippus scalaris*, Siberia (Troitsky, 1914); *A. microptera*, W. Siberia (Moritz, 1915); *Calliptamus italicus*, Siberia (Bezrukov, 1922).

Systoechus autumnalis, Pall.—*D. maroccanus*, Crimea (Stepanov, 1881, figures); various grasshoppers, Eastern Siberia (Ingenitsky, 1898); *Chorthippus scalaris*, *Gomphocerus sibiricus*, Siberia (Troitsky, 1914); *A. microptera*, *Dociostaurus kraussi*, *D. albicornis*, W. Siberia (Vorontsovsky, 1926).

S. ctenopterus, Mikan.—*G. sibiricus*, *C. scalaris*, Siberia (Bezrukov, 1922).

S. leucophaeus, Meig. ?—*D. maroccanus*, Crimea (Stepanov, 1881, bionomics, description of pupa, figures); *C. italicus*, Russia (Lindeman, 1902). Specific determination in both records doubtful.

S. oreas, O. S.—*Camnula pellucida* and other grasshoppers, British Columbia (Treherne and Buckell); *C. pellucida*, California (Riley, 1880, description of larva, pupa, figures).

S. socius, Wlk.—*Colemania sphenarioides*, S. India (Fletcher, 1916).

S. vulgaris, Loew.—*Camnula pellucida*, British Columbia (Treherne and Buckell).

Systoechus sp.—*D. maroccanus*, Transcaucasia; *L. migratoria*, Astrachan (Portchinsky, 1894, figure of larva).

Aphoebantus (*Triodites*) *mus*, O. S.—*Camnula pellucida*, California (Riley, 1880, description of larva and pupa, figures).

All the above feed directly on the eggs of the respective species of ACRIDIDÆ, but there is one species, *Argyramoeba zonabriphaga*, Portch., which occurs also in the egg-pods, but feeds not on the eggs, but on the larvæ of other Bombyliids and of *Mylabris* (Portchinsky, 1895; Troitsky, 1914). The larva of this fly is very similar to that of *Anthrax fenestratus*, but differs from the larvæ of all Bombyliids by the presence of a round sucker on the posterior end of its body; by means of this, the larva attaches itself to its victim and then sucks it out through the mouth. It is not impossible that some other species of Bombyliids, recorded as bred from egg-pods, are also secondary parasites.

Other Flies, parasitising the Egg-pods.—*Schistocerca gregaria* in Algeria (Künckel) and in Egypt (Min. Agric. Egypt, 1916) is liable to the attacks of the fly, *Stomatorrhina* (*Idia*) *lunata*, F., of the subfamily MUSCINÆ (Fig. 52); this lays its eggs on the egg-pods of the locust, reaching them through crevices in the ground; the eggs are laid by means of a long ovipositor, which is drawn in when not in use. Only eggs laid in hard soils are subject to its attacks, because the fly is unable to reach them if the soil is loose.

A part of some importance in the destruction of eggs is sometimes taken by larvæ of small flies of the family ANTHOMYIIDÆ, to which belong several well-known pests of vegetables with succulent roots. Normally the larvæ of these flies feed on the roots of plants, occasionally on decaying vegetable matter, etc., so that they cannot be considered specific enemies of ACRIDIDÆ, the eggs of which are apparently devoured when met with accidentally. The following species of Anthomyiids have been recorded from egg-pods:

Anthomyia radicum, L.—*Locusta migratoria*, Ukraine (Stepanov, 1881).

A. cana, Macq.—*Dociostaurus maroccanus* and *Schistocerca gregaria*, Algeria (Künckel).

A. rubrofasciata, Macq.—*Nomadacris septemfasciata*, Réunion (Bordage, 1914).

Chortophila cilicrura, Rond.—D. *maroccanus*, Anatolia (La Baume, 1918); *Schistocerca paranensis*, Argentina (Künckel, 1907).

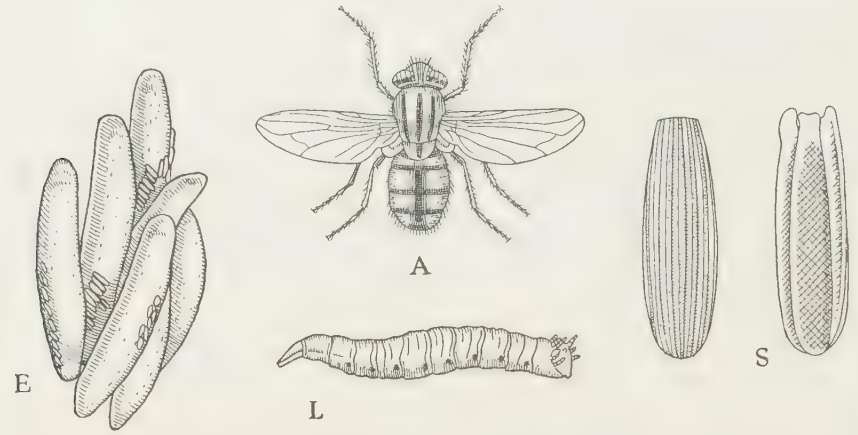

FIG. 52.—Metamorphosis of *Stomatorrhina lunata*, F.—E, group of eggs of the fly on locust eggs. —S, single eggs enlarged.—L, larva.—A, adult (after Künckel).

Pegomyia fusciceps, Zett. (*Anthomyia angustifrons*, Meig., *A. radicum* v. *calopteni*, Riley).—*Melanoplus spretus*, N. America (Riley, 1878); *Schistocerca paranensis*, Argentina (Lahille, 1907).

Künckel (1907) states that all records of Anthomyiids from egg-pods of ACRIDIDÆ must be referred to one practically cosmopolitan species, *Chortophila cilicrura*, Rond. (Fig. 53). He states that in Argentina the female flies came in numbers into his tent where he kept locust eggs in boxes and tried to get into them; thrusting the ovipositor into cracks in the boxes, they laid very agile living larvæ that immediately began to run, searching for locust eggs. Other observers state that several larvæ may occur in one pod, and this comprises all the information we possess on these enemies of ACRIDIDÆ.

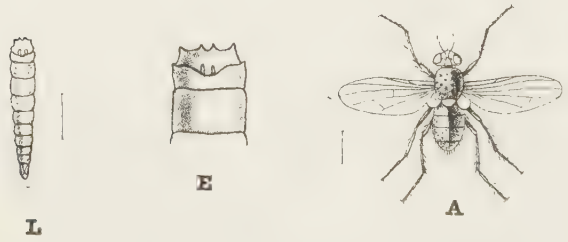

FIG. 53.—*Chortophila cilicrura*, Rond.—L, larva.—E, end of abdomen of larva.—A, adult (after Künckel).

Probably only occasional enemies of the egg-pods are larvæ of the small fly, *Siphonella palposa*, Fall., of the family CHLOROPIDÆ (to which belong several important pests of crops, *e.g. Oscinella frit*). They have been found several times in the egg-pods of smaller species of grasshoppers in Russia. Thus, Bezrukov (1922) bred them from the egg-pods of *Stenobothrus nigroma-*

culatus in Siberia, and Shapinsky (1923) observed an extensive infestation of egg-pods of *Chorthippus biguttulus* and *C. apricarius* by larvæ of this fly near Moscow. The last-named author gives some information on the bionomics of this species, stating that as many as 12–20 larvæ may be found in one egg-pod, and that the number of larvæ actually exceeded in some cases the number of eggs in the pod. Unfortunately, the larva has never been described.

Other families of flies also supply some useful enemies of Acridid eggs, though it is difficult to say whether their parasitic habits are normal, or whether the cases recorded are accidental. Thus the Leptid, *Chrysopila nubecula*, Fall., occurs in the pods of *Dociostaurus maroccanus* in Algeria (Künckel); the Therevid, *Psilocephala lateralis*, Ad., was bred from the pods of *Camnula pellucida* in British Columbia (Treherne and Buckell); and the Syrphid, *Volucella bombylans*, L., has been recorded from those of *D. maroccanus* in Anatolia (La Baume, 1918), but this last record seems very doubtful.

It is remarkable that the families Tachinidæ and Sarcophagidæ, which supply, as we shall see later, some of the most serious enemies of adult Acrididæ, have also been observed as parasites in the egg-pods, though the records are not abolutely convincing and require confirmation. Thus, Stefani Perez (1913) records that from the egg-pods of *D. maroccanus* in Sicily he often bred *Tachina larvarum*, L., a common parasite of various caterpillars. Kelly (1914) quotes a case of breeding from the egg-pods of *Melanoplus spretus* the fly, *Sarcophaga kellyi*, Aldr., which also parasitises adult grasshoppers. Nikolsky (1925) states that he once found a full-grown larva of *Wohlfahrtia balassogloi*, Portch., also a parasite of adult locusts, in the egg-pod of *L. migratoria*. Finally, in the report of the Ministry of Agriculture, Egypt (1916), we find a record that the eggs of *Schistocerca gregaria* were attacked by larvæ of *Sarcophaga falculata*, Rond. (?). In South Africa *Wohlfahrtia euvittata*, Villn., has been recorded as a parasite of the eggs of *Locustana pardalina* (Journ. Dept. Agr. S. Africa, 11, 1925, p. 381).

Fig. 54.—*Scelio nikolskyi*, Ogl. Much enlarged (after Nikolsky).

Hymenopterous Parasites of the Eggs.—It is a very remarkable fact that there are no parasites of Acrididæ in any stage amongst the two great Hymenopterous groups of Ichneumonidæ and Braconidæ, several old records of this kind being obviously incorrect. On the other hand, amongst the minute insects of the Chalcidoidea and Proctotrupoidea we already know a number of specific parasites of Acridid eggs, while there is every reason to expect further discoveries of the same kind.

The best-known of them and, perhaps, the most important are representatives of the family Scelionidæ (Proctotrupoidea), the majority of recorded species belonging to the world-wide genus *Scelio*. The species of this genus are very small, shining black insects, 4–5 mm. in length (Fig. 54). Various observers record that the number of females usually greatly exceeds that of the males, which seems to indicate the possibility of, at least, occasional

parthenogenesis. In Australia, where these parasites are particularly numerous, they have been observed in masses running over the ground in the places where the eggs of locusts have been laid (Dodd, 1913). Vinokurov (1927) recorded similar observations in Siberia, where he counted up to 20 parasites in 15 minutes over an area of 0·2 square metres. The last-named author was the first to describe how grasshopper eggs are infested by the parasite. According to him, when a female parasite running over the ground encounters an ovipositing grasshopper, it comes close to its abdomen, even touching it with its head, and awaits the end of oviposition ; sometimes two, or even four, parasites may be seen waiting in this way. As soon as the grasshopper has finished ovipositing and the hole is filled in, the parasite digs into the ground, reaches the egg-pod, turns head upwards, and infests the eggs one by one through the walls of the pod, by means of its relatively very long ovipositor (in *Scelio javanica* it is three times the length of the body), which is normally not visible, being concealed within the abdomen. Vinokurov's observations have shown that only freshly laid eggs are liable to infestation, while those laid more than 30 minutes previously do not attract parasites. This is due to the fact that the parasites proved to be attracted not by the eggs themselves, but by the foamy secretion of the accessory glands emitted during oviposition, and only so long as the secretion is not dry. In some laboratory experiments the parasites paid no attention to eggs freed from the secretion, but were attracted at a distance of 10 cm. by the latter in the absence of eggs.

It is probably due to the attraction by the secretion of the accessory glands that the females of some species of *Scelio* have been observed firmly attached by their mandibles to adult Acrididæ. Facts of this kind have been recorded from North America, and Brues (1917) figures a female of the wingless Indian grasshopper of the genus *Orthacris* (he calls it, by an obvious mistake, *Colemania sphenarioides*), bearing three parasites on its body ; I have also found a specimen of *Orthacris* in a collection with a parasite which firmly gripped with its mandibles the membrane between the segments of the abdomen of its host. In this way the parasite may be carried about by the grasshopper until the moment comes for the latter to lay its eggs ; presumably, these parasites attach themselves only to female grasshoppers that are quite ready for oviposition. The important point about this habit is that the parasites are carried by their hosts to wherever the eggs will be laid.

As I have mentioned above, these egg parasites are, apparently, more abundant in Australia than in any other country ; they are, however, also known from elsewhere, and it seems certain that they are more common than has been suspected, but that they are overlooked owing to their small size. The total number of known species of the genus *Scelio* is very large, but only a few of them are definitely recorded as parasites of eggs of Acrididæ. A list of them is given below, but I must specially warn readers that the names of the Australian hosts in it are very doubtful, since most of the Australian injurious Acrididæ have been recorded under incorrectly applied names (see below, p. 203), so that it has become quite impossible to decide what species

is meant in each case ; all doubtful names are given in the list in inverted commas.

List of Scelionid parasites of the eggs

Scelio australis, Frogg.—"*Locusta australis*" (probably *Ausiracris* sp.), Australia (Froggatt, 1910, figure of the adult).

S. calopteni, Riley.—*Melanoplus atlanis*, United States (Ashmead, 1893) ; *Melanoplus* spp., British Columbia (Treherne and Buckell).

S. chortoicetes, Frogg.—*Chortoicetes terminifera*, Australia (Froggatt, 1910).

S. froggatti, Crawf.—*C. terminifera* (Crawford, 1911), "*Locusta danica*" (probably *Gastrimargus musicus*), Queensland (Dodd, 1913).

S. fulgidus, Crawf.—"*Locusta australis*, Brunner," N. S. Wales (Crawford, 1911).

S. hieroglyphi, Gir.—*Hieroglyphus banian*, S. India (Ramakrishna Ayyar, 1920).

S. howardi, Crawf.—*Nomadacris septemfasciata*, Zambezi (Crawford, 1911).

S. hyalinipennis, Ashm.—*Melanoplus differentialis*, *Schistocerca obscura*, Mississippi (Morgan, 1901).

S. indicus, Ashm.—*Patanga succincta*, India (Lefroy, 1906).

S. javanica, Roepke.—*Valanga nigricornis*, Java (Roepke, 1916 ; bionomics, figure of imago).

S. luggeri, Riley.—*Melanoplus*, N. America (Ashmead, 1893).

S. nikolskyi, Ogl.—*Locusta migratoria*, Turkestan (Ogloblin, 1927).

S. oedipodae, Ashm.—"*Oedipoda*," Virginia (Ashmead, 1893) ; *Melanoplus differentialis*, *Schistocerca obscura*, Mississippi (Morgan, 1901).

S. ovi, Gir.—Apparently *Locusta danica*, Queensland (Girault, 1913).

S. ovivorus, Riley (*famelicus*, Riley).—*Dissosteira carolina*, United States (Riley, 1878).

S. oxyae, Gir.—*Oxya*, S. India (Ramachandra Rao, 1921).

S. pulchellus, Crawf.—? *Austroicetes pusilla*, N. S. Wales (Crawford, 1911).

S. uvarovi, Ogl.—*Locusta migratoria*, S. Russia (Ogloblin, 1927).

S. venezuelensis, Marsh.—*Schistocerca* sp., British Guiana (Bodkin and Cleare, 1919).

Lepidoscelio ? viatrix, Brues.—*Orthacris* sp., S. India (Brues, 1917).

Apart from Scelionids there are other egg parasites, but very little is known about them. Thus from the eggs of *Oxya* in S. India two Chalcidoid parasites were bred, *Anastatus coimbatorensis*, Gir., and *Tumidiscaphus oophagus*, Gir. ; the latter has a secondary parasite, *Aximopsis tumidiscaphi*, Gir., and is remarkable for the fact that as many as 17–21 parasites can emerge from a single grasshopper egg (Ramachandra Rao, 1921).

Berezhkova (1924) discovered in the eggs of *Chorthippus scalaris* in Siberia a very interesting egg-parasite of the genus *Prophanurus* (as I am informed by Mr. N. F. Meyer, who has seen the specimens, but was unable to name the species). The eggs in nature were so heavily infested that in many places no hoppers emerged at all. In many cases all the eggs in one pod were infested.

In one egg it was possible to find at first several (up to nine) larvæ of the parasite, but never more than one adult parasite emerged from each grasshopper egg, the others, apparently, having been eaten by the surviving larva. The infested eggs can be recognised by the absence of the eyes of the hopper embryo, which are plainly visible in mature and sound eggs. The author thinks that the cycle of development of the parasite is as follows : Copulation takes place in July, when the grasshoppers oviposit, and the eggs are infested when laid, though it was not observed how this happens ; the larvæ of the parasite pass through two stages (which are fully described but not figured by the author) and pupate at the end of the next spring. The adult parasites, when emerging, make their way through the walls of the pods, and these subsequently appear as if pierced by gun-shot.

Apart from *Prophanurus*, Berezhkova mentions three more Hymenopterous egg-parasites of the same grasshopper, but their determinations, or details of their bionomics, have never been published. Shapinsky (1923) also found some Chalcidoid larvæ in the eggs of *Chorthippus* near Moscow, but failed to breed the adults.

Red Mites.—Every entomologist, who has had to deal with ACRIDIDÆ, knows the small red mites that may be found, sometimes in great numbers, attached to the body of adult grasshoppers or their larvæ. Some information on these mites, sometimes accompanied by more or less fantastic specific names, can be found in nearly every paper on locusts, but our real knowledge, even of the systematics of these parasites, is exceedingly inadequate, while the data on their bionomics exist only in respect of one or two species, and these are usually attributed to the others. The study of the systematics of the red mites is greatly hampered by the fact that it is the larval stages that occur on ACRIDIDÆ, while the adults are free-living and differ considerably from the larvæ ; as a consequence, many species have been described only from adults and others only from larvæ ; the connection between the two can be established only by breeding, and this is very seldom done.

A fairly complete outline of the life-history of an American species, *Eutrombidium locustarum*, Walsh (according to Oudemans, 1913, this is a synonym of the common European *E. trigonum*, Herm.), has been given by Howard (1918).

The adult mites (Fig. 55, M ; *Podapolipus grassii*, Berl., ♂) occur on, or in, the ground very early in spring ; appearing in the first warm days, they immediately set out in quest of egg-pods. Sometimes they appear in such numbers that the ground is covered with them and looks red. To find the eggs, the mites dig into the soil and enter the pods, sometimes several of them into one, though more often only one mite is found in a pod. The egg-shells are then pierced by their sharp mandibles, and the contents sucked out. There is no direct evidence as to how many eggs a mite must suck before attaining sexual maturity, but apparently three or four are sufficient. No preference for the eggs of certain species of ACRIDIDÆ was observed, and the mites can become mature in cages where there are no eggs, probably by feeding on the moisture of a soil rich in humus. An engorged female doubles its size, and

the shape of its body becomes very different, owing to the smoothing out of the transverse furrows (Fig. 55, F).

Copulation takes place in the pod, into which several males sometimes enter together, if it contains a female. For oviposition, the female makes in the

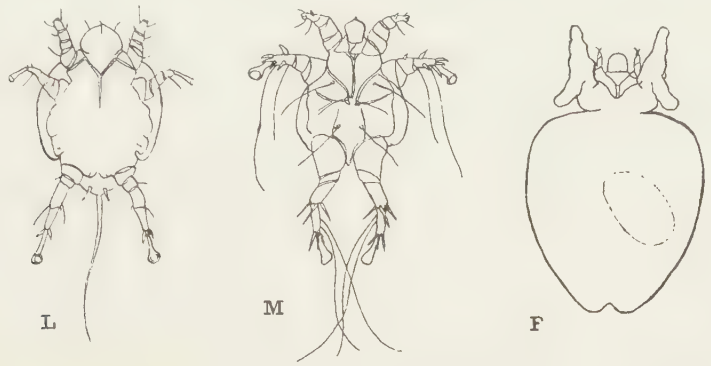

Fig. 55.—*Podapolipus grassii*, Berl.—M, adult male.—L, larva.—F, engorged female (after Berlese).

soil from about $\frac{1}{2}$ to 1 inch under the surface, a small cell with smooth walls, in which the eggs are laid in a mass of 300–700, compactly glued together. The larvæ emerge after 24–30 days ; they scarcely differ from the adults (Fig. 55, L). The newly-hatched larvæ run very actively on the ground looking for Acridids, and, on finding a victim, attach themselves to it by their mandibles. They can be found on all stages of grasshopper larvæ as well as on the adults. In the case of the latter, the mites usually attach themselves to the veins of the hind wings (Fig. 60), but on the hoppers they occur in various places : between the segments of the abdomen and of the thorax, on the tarsi, near the mouth, and often under the wing rudiments. On one hopper there may be from one and up to a hundred mites ; on the wings of the adults they may be so numerous that the insect is not only unable to fly, but even to close its wings. It is entirely unknown how the mite finds a new host after having been shed together with the old skin during a moult.

Fig. 56.—A larva of *Eutrombidium trigonum*, Herm. (after Oudemans).

After becoming attached, the larva begins to increase rapidly in size and loses all resemblance to its old self (Fig. 56 ; *Eutrombidium trigonum*). The fully engorged larva drops from its host and burrows into the soil, where it transforms into a nymph that is very similar to the adult mite. The nymphs find the egg-pods (which are laid by this time, the end of the summer), engorge on the eggs, and then transform into the adult stage, which hibernates.

Recent unpublished observations on *Eutrombidium debilipes* parasitising *Locusta migratoria* in N. Caucasus, made by Mr. N. Olusfiev and kindly communicated to me, show that the general cycle of development in this species is similar to that described above. It must be remembered, however, that as representatives of many genera, belonging to three different families, have been recorded as parasitic on ARCIDIDÆ, and as their bionomics must vary a great deal, it would be unsafe to apply the above data to all of them.

The value of these mites as a factor regulating the numbers of ACRIDIDÆ is very difficult to determine at the present stage of our knowledge. Their effect on the adults and on the hoppers can scarcely be regarded of importance, though when the infestation is very great, this may have some effect on the general activity of the host ; for the migrating species the presence of a large number of mites on the wings may to a certain extent influence migration. The part taken by the mites in the destruction of eggs seems much more important, but this point in their bionomics has been less investigated than any other ; according to unpublished observations by Miss A. A. Popova (communicated by Mr. I. N. Filipjev), up to 30–40 per cent. of the eggs of *Locusta migratoria* in N. Caucasus may be destroyed by mites.

A thorough study of these mites is urgently needed, and attention must be paid, first of all, to their systematics, in order to be clear as to the number of species involved and their differences in all stages. The mere collecting of the mites found attached to ACRIDIDÆ is not very helpful in this respect, since they are in the larval stage, and it is always necessary to try to obtain nymphs and adults. This can be attained by keeping the Acridids, infested with mites, alive in a cage until the mites drop from them for further transformation. Equally important is the collection of mites in the egg-pods,where the nymphs and the adults may be found.

When making bionomic observations, it is imperative to preserve a part of the material from each stage for systematic purposes as there is always a chance that more than one species is involved. It must be never forgotten that the systematics of the mites are based on certain minute characters, and superficially similar creatures may actually belong to very different groups.

List of red mites parasitic on Acrididæ

Family TROMBIDIIDÆ.

Eutrombidium trigonum, Herm.—On hoppers of *Calliptamus italicus*, *Oedipoda coerulescens*, *Parapleurus alliaceus*, Europe (Oudemans, 1913 ; this author considers this species synonymous with the next one, but Berlese, 1912, separated them by a number of characters).

E. locustarum, Walsh.—In egg-pods and on adults of various grasshoppers (Howard, 1918, bionomics, figures ; Hunter, 1899 ; see the remark under the preceding species).

E. debilipes, Leon.—On adults of *Locusta migratoria*, Russia (Leonardi, 1910, description, figures ; the latter are, according to Oudemans, 1913, incorrect ; Nikolsky, 1925, bionomics).

Allothrombium fuliginosum, Herm.—Acrididæ, Russia (Portchinsky, 1894 ;

no definite information is given by the author, and the identification seems unreliable).

Sericothrombium holosericeum, L.—"*Acridium* sp.," Europe (Berlese, 1913 ; Oudemans, 1913, considers this a synonym of *E. trigonum*).

Parathrombium paolii, Berl.—In the egg-pods of *Dociostaurus maroccanus*, S. Italy (Berlese, 1918).

Trombidium grandissimum, Koch.—On hoppers of *Patanga succincta*, India (Lefroy, 1906 ; Berlese, 1893, considers this a synonym of *T. tinctorium*, F.).

T. acridii-peregrini and *T. elegans*.—These two species are recorded as parasites of *Schistocerca paranensis* in Argentina by Bruner (1898), but they have apparently never been described.

Fig. 57.—A larva of *Erythraeus phalangioides*, Deg. (after Oudemans).

Family Erythræidæ.

Achorolophus epigaeus, Berl.—In the egg-pods of *Dociostaurus maroccanus*, Italy (Berlese, 1918).

A. ignotus, Oudem.—On various insects in Europe and on *Melanoplus bivittatus* in America (Oudemans, 1913).

A. sp.—On adults of *Schistocerca paranensis*, Mexico (Dampf, 1925).

Erythraeus areolatus, Träg.—On a grasshopper, E. Africa (Trägårdh, 1908).

E. braunsi, Oudem.—On *Acrida* sp., W. Africa (Oudemans, 1910).

E. jaegerskioldi, Träg.—On an Acridid, Sinai (Trägårdh, 1905).

E. kibonotensis, Träg.—On an Acridid, E. Africa (Trägårdh, 1908).

E. phalangioides, Deg. (Fig. 57).—*Calliptamus italicus*, "*Stenobothrus* spp.," etc., Italy (Berlese, 1893) ; *Oedipoda coerulescens*, Europe (Oudemans, 1913).

Family Tarsonemidæ.

Podapolipus aharonii, Hirst.—*Tropidopola longicornis*, Fieb., Palestine (Hirst, 1921).

Podapolipus berlesei (author ?).—*Schistocerca paranensis*, Argentina (Lahille, 1907 ; the species has apparently never been described).

P. grassii, Berl.—On the adults of *Locusta migratoria*, in masses, Italy (Berlese, 1900) ; on " a locust," Australia and Java (Berlese, 1911).

Some Less Important and Accidental Enemies of Egg-pods.—To this category belong, first of all, certain birds, such as cranes, rooks, etc., which during the years of the mass appearance of locusts feed on their eggs fairly regularly, digging for them in the ground. While in some cases the birds may seriously reduce the numbers of locusts, their general importance in that respect must not be over-estimated.

Many carnivorous larvæ of bettles of various families have been recorded in the literature as enemies of the egg-pods. Perhaps the best known is the " Champi " of South American writers, a Lamellicorn beetle, *Trox suberosus*, F. (Fig. 58), which has been recorded as doing a great deal of damage to egg-pods of *Schistocerca paranensis*, the beetles appearing in large numbers in places where the eggs are laid and attacking them ; the larvæ of this beetle are also said to feed on locust eggs (Conil, 1881 ; Bruner, 1898). These observations are contradicted by Berg (1898), who states that the beetles in captivity refused to touch either fresh or decaying locust eggs, but fed on the dry eggs and on the outer cover of the pods ; the larvæ, which he received on several occasions as those of " Champi," were larvæ of flies. He concludes that *Trox* may do only indirect damage to egg-pods by destroying the outer walls of the egg-pods and exposing the eggs ; this statement seems to agree with the general habits of other species of the genus *Trox* which all feed on dry animal products (hides, bones, etc.), and further evidence is necessary to decide on the actual interrelations between locusts and the " Champi."

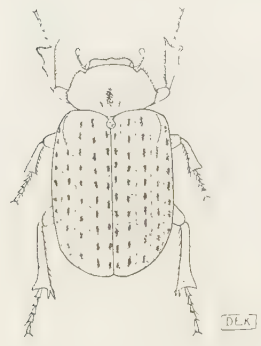

Fig. 58.—*Trox suberosus*, F. Enlarged (original).

Amongst other families of beetles, records are known of larvæ of Elaterids (wireworms), Telephorids, Carabids, etc., occasionally destroying eggs of Acrididæ. While in some cases the larvæ appear in large numbers and cause the destruction of a very great proportion of the egg-pods, there is no reason to suggest that any of these beetles may be regarded as specialised enemies of Acridids, and all attacks must be explained as accidental.

Equally accidental, though often serious, enemies of egg-pods are some ants (particularly *Myrmecocystus viaticus*, F., and *Aphaenogaster subterraneus*, Latr.).

Specialised parasites of the eggs probably include certain Nematodes. Rekalo (1884–1885) recorded them in the eggs of *Locusta migratoria* on the Danube, but the species has not been determined ; Dampf (1925) also observed Nematodes of the genus *Rhabditis* in the eggs of *Schistocerca paranensis* in Mexico.

Egg-pods of *Patanga succincta* in India have been recorded to be damaged by a small Oligochæte worm, *Henlea lefroyi*, Bredd. (Breddin, 1907), but there is no reason to think that this is a special enemy of the eggs.

Fungous Parasites of the Eggs.—Cases of fungous diseases of egg-pods have often been recorded in the literature, but a proper mycological study of the fungi able to attack living Acridid eggs has never been attempted, and only Krassilschik (1886) has given some definite information on the fungi that destroy eggs of *Locusta migratoria* in South Russia. That author states that he observed up to 40 per cent. of the eggs infested by fungi, which he refers to the genus *Isaria* (*I. farinosa*, *I. destructor*, and two undetermined species); it may be mentioned that the name *Isaria* conveys very little, since it has been the custom to relegate to it almost any indefinite fungoid organism. There is no evidence, moreover, that the fungi in question were actually responsible for the destruction of the eggs; it is quite possible that they only attack eggs damaged by other enemies. In my own experience I have often met with egg-pods covered with mycelium, but in all cases it has been present only on the cover of the pods and between the eggs, which remained sound. La Baume (1918) describes cases of serious infestation of eggs of *Dociostaurus maroccanus* in Anatolia by fungi; amongst the latter several forms were found, the commoner being a species near *Fusarium acridiorum*, which it was possible to cultivate on gelatine, though all attempts at artificial infestation of eggs failed. All this information only shows that the study of the fungoid enemies of eggs is a task for future investigators.

Krassilschik (1886) also records the presence of some Coccidia in the eggs of *Locusta migratoria*, but their rôle is not clear; in any case, no harm to the eggs was noticed, and it may be suggested that these organisms were merely harmless symbionts.

Parasites and Enemies of Hoppers and Adults

This group includes a large number of various organisms, ranging from mammals to gregarines and bacteria, but perhaps it would be wise to begin with certain flies, the larvæ of which live as true parasites inside the body of Acrididæ, as these are probably the most important of all.

Larviparous Flies.—The presence of fly maggots in the body of Acrididæ was known very long ago, but only relatively recently has more exact information been obtained on the bionomics of these parasites and on their interrelations with their hosts.

The vast majority of species of flies bred from Acrididæ belong to the subfamily Sarcophaginæ, of the family Tachinidæ, and practically all sufficiently studied species have proved to be larviparous, as we shall see later.

In external appearance all these flies are very similar to one another, and they resemble the common house fly more or less (Fig. 59).

Relatively very complete biological data exist with regard to two species, the European, *Blaesoxypha lineata*, Fall., recorded by several authors as a parasite of locusts (Portchinsky, 1894; Baranov, 1924, 1925), and the North American, *Sarcophaga kellyi*, Aldr. (Kelly, 1914).

The adult flies may be seen sitting on the stems and leaves of plants, on flowers, stones, etc., or simply on the ground; *Blaesoxypha* is very sluggish at this period and scarcely moves. This is changed, however, when the flies

become sexually mature. After pairing, the eggs develop into small larvæ which hatch inside the oviduct, the latter acting as a uterus. When the oviducts are filled with larvæ, the females become very active, and their movements are remarkable for their jerkiness ; a female that is quietly sitting on a plant when an Acridid flies past it, suddenly darts after it with a sharp buzzing sound, seems to strike it from underneath, and the Acridid usually drops to the ground. A careful examination of the Acridid enables one to find one or more newly born fly larvæ generally on the underside of the wings, and these crawl very rapidly towards the base of the latter. Sometimes the larvæ are found on the lower surface of the abdomen, or the sternum. In all cases the larvæ soon reach one of the thin membranes between the segments and burrow inside the body. This latter action is made possible by the presence on the head of the larva of sharply pointed mandibles and of rings of bristles on its body which serve as a support when it burrows.

The act of infestation is easily observed in nature, since it is common to see an Acridid pursued by several flies when taking wing. Interesting observations by Kelly (*l.c.*) prove that it is the rapid movement of an Acridid that induces the fly to dart after it ; he has often observed the flies pursuing and laying a larva on Lepidoptera, on a Cicada, and even on balls made of paper and thrown over a sitting fly. This inclination to pursue all rapidly moving objects seems to be the cause of flies being carried in the swarms of locusts ; I once had an opportunity of observing very large numbers of the flies amongst a swarm of locusts, which had just settled down after an emigration flight that had begun hundreds of miles away ; the flies must have come with the swarm, since their presence in such large numbers could not be explained in any other way.

Fig. 59.—*Sarcophaga kellyi*, Aldr. Enlarged (after Kelly).

In the case of hoppers, the larvæ are also deposited, according to Kelly, only when the hoppers move ; Baranov, however, observed that in cages the flies often laid their larvæ simply by jumping on a resting hopper.

In other species of flies the larva is laid between the genital valves of the host, by means of a long extensible ovipositor which is not developed in *Blaesoxypha lineata ;* this observation was made on *B. erythrura*, Mg. (Portchinsky, 1894), and *B. grylloctona*, Loew (Loew, 1861).

Portchinsky believed that only adults are liable to the attacks of the flies, but Michelson (1922) found fully grown larvæ of flies already in the hoppers of the third stage, indicating that infestation may occur in as early as the second, or even the first stage of the hoppers. Recent information collected by Mr. N. G. Olsufiev (not published, but kindly communicated to me by the author

through Mr. I. N. Filipjev, acting Director of the Russian Bureau of Entomology) indicates that *B. lineata*, contrary to the views of Baranov, is a specialised parasite of adult locusts, but there are other species of the same genus that parasitise the hoppers only, or both hoppers and adults.

The number of larvæ inside one Acridid may reach ten (Michelson, *l.c.*), but it must be assumed that this is due to repeated attacks by several female flies.

The very important problem of how the larva feeds inside its host is not yet quite clear. It is usually assumed that the larva feeds mainly on the fat-body, and devours more vital organs only towards the end of its development. It is probable that various species of flies have different feeding habits, and that, at least in some of them, must occur what Pantel (1912) found in a Tachinid, *Thirixion halidayanum*, Rond., parasitising stick insects of the genus *Leptynia* in Spain ; here the fly larva does not feed even on the fat-body, but merely on the blood of its host, *i.e.* without causing any direct injury to the latter.

The larva passes two larval stages inside the host, not counting the one in which it enters it ; in these two later stages the larva is similar to other fly maggots, and the stages can be differentiated by their size and that of the strongly chitinised mouth-parts. The whole larval development in *B. lineata* occupies four to six days, and the larva then leaves the host through one of the membranes between the segments or through the anal opening. It then immediately burrows into the ground and pupates in a barrel-shaped, reddish-brown puparium. The pupal stage lasts about seventeen days. Baranov was unable to find out the exact number of generations during a season, but Kelly records five to six of them.

The question of the practical importance of larviparous flies is not easy to answer. Indeed, there is obviously a marked divergence in the effect on the host between different species of flies. Olsufiev (*in litt.*) records that *B. lineata* is practically harmless, since locusts infested by its larvæ appeared quite normal, ate as usual, and even paired and laid eggs. Other species of *Blaesoxypha*, observed by him, proved to be much more effective in causing the death of locusts. Even in the case observed by Pantel in stick insects, the larva, though not feeding on any tissue of the host, caused degeneration of the genital products. It is clear that generalisations in this respect are dangerous and that the inter-relations of each species of these flies with its host must be studied separately.

The percentage of infestation by these parasites is often very high, and records of a 100 per cent. infestation of a swarm are not rare in the literature, but the foregoing considerations make it impossible even in such cases always to expect a complete annihilation of the swarm, though this sometimes happens.

The method of infestation makes it understandable that these parasites, or at least some of them, are not very selective as regards their hosts ; indeed, the records of breeding show that many species parasitise various Acrididæ, while some of them occur in other insects as well. Consequently, these parasites can develop throughout a season on various hosts, and this is an obvious advantage to them.

In their turn the flies become victims of certain secondary parasites, mostly

of the Hymenopterous genus, *Brachymeria* (*Chalcis*). The larvæ of these live inside the fly larvæ, which latter undergo all their metamorphoses in an apparently normal way until the *Brachymeria* emerges from the puparium. The actual method of infestation is somewhat difficult to understand. Stefani Perez (1913) observed *B. dallmani*, Th., attacking a Moroccan locust on which, in spite of its struggles, it apparently laid an egg by inserting its ovipositor into the mesonotum. Vinokurov (1927) made a similar observation on *B. femorata*, Dall. It is difficult to believe that *Brachymeria* infests with its eggs the larva of the fly which is inside the body of the locust; more probably the egg of the hyperparasite is laid in a haphazard manner (sometimes perhaps even on a locust that is not infested with the fly larva), and its larva has to find its host. In the case of some smaller hyperparasites this seems very probable, because in *Perilampus*, which is also known as a hyperparasite of the locust flies, a special first stage of the larva, called the planidium and adapted for the purpose, has been found in a long-horned grasshopper of the genus *Xiphidium* (Ford, 1922).

Before giving a list of the species of larviparous flies, I should state that it is based entirely on records in the literature and that these differ greatly in their scientific value. In many cases it is impossible to find out on what authority a specific identification of the parasite is based, and a considerable proportion of such records seem more or less doubtful. With regard to North American records, I rely on the work by Aldrich (1916), who checked many of the original records; I have also accepted his views on the systematics and synonymy of species of SARCOPHAGIDÆ. Certain corrections in the identifications of Palæarctic species recorded as parasites of ACRIDIDÆ have been made by Baer (1920–1921), especially in respect of the records by Künckel. In other cases I had no option but to quote the original records. Even when the latter are correct as regards the specific names of the parasites, it is not always clear whether the species recorded were actually bred under conditions definitely proving their parasitic habits; it must not be forgotten that many SARCOPHAGIDÆ and allied flies deposit their larvæ on dead animals, decaying organic matter, etc., so that it is always possible that dead ACRIDIDÆ collected in the field, or which have died in laboratory, may be infested by larvæ of some flies after death. There is no doubt that many cases of this kind are recorded in the literature as cases of parasitism.

Following Aldrich, I record all the species of *Sarcophaga* s.l. under this genus, giving subgeneric name (when certainly known to me) in brackets. The genera in the list are in systematic, and the species under each genus in alphabetical order.

List of larviparous flies parasitising Acrididæ

Agria affinis, Fall.—*Schistocerca gregaria*, Algeria (Künckel).

Oedematocera dampfi, Aldr.—*Sch. paranensis*, Mexico and Guatemala (Aldrich, 1927, 1927*a*; Greene, 1927, figures of larva and puparium; Townsend, 1928, founded a new genus, *Schistocercophaga*, for this species).

Wohlfahrtia balassogloi, Portch.—*Locusta migratoria*, Russia (Rossikov, 1899); *L. migratoria*, *C. italicus*, Russia (Portchinsky, 1916; figures of larva and imago).

W. brunneipalpis, Macq.—*Locustana pardalina*, S. Africa (Journ. Dept. Agr. S. Africa, 11, 1925, p. 381).

Sarcophila latifrons, Fall.—*Locusta migratoria*, Turkestan (Rossikov, 1899); *Chorthippus albomarginatus*, E. Siberia (Vinokurov, 1927).

Brachycoma acridiorum, Weyenb. (*Sarcophaga minuta*, Lah.).—*Schistocerca paranensis*, Mexico, S. America (Weyenbergh, 1876; Berg, 1898; Lahille, 1907; Brèthes, 1912; Aldrich, 1927*a*).

B. acridiorum var. *obscurior*, Lah.—*S. paranensis*, Argentina (Lahile, 1907).

Sarcophaga aculeata, Aldr.—*Melanoplus atlanis*, *M. spretus*; also attacking *Schistocerca americana* in flight, N. America (Aldrich, 1916).

S. assidua, Wlk.—*Melanoplus differentialis*, N. America (Morgan, 1901; according to Aldrich, 1916, identification doubtful).

S. atlanis, Aldr.—*M. atlanis*, N. America (Aldrich, 1916).

S. atropos, Meig., see *S. striata*, F.

S. aurifrons (?).—" Locusts," Australia (Froggatt, 1910).

S. brevicornis, Vill.—Grasshoppers, E. Siberia (Vinokurov, 1927).

S. caridei, Brèthes (=*Nemoraea acridiorum*, Conil, Lahille; *angustifrons*, Aldr.).—*S. paranensis*, Argentina (Massini, 1919; Conil, 1881; Lahille, 1907); Mexico (Aldrich, 1927a).

S. cimbicis, Town.—*M. differentialis* (Hunter, 1899), *Chorthophaga viridifasciata*, N. America (Kelly, 1914). According to Aldrich, both these records are erroneous, but it is impossible to refer them to other species.

S. clathrata, see *S. ungulata*.

S. cruentata, Meig.—*Dociostaurus maroccanus*, Algeria (Künckel).

S. davidsoni, Coq.—Attacking flying grasshoppers, N. America (Aldrich, 1916, p. 302).

S. (*Blaesoxypha*) *erythrura*, Meig.—Acrididæ, Russia (Portchinsky, 1894). (Mr. N. Olsufiev writes to me that there are several species under this name in Portchinsky's collection.)

S. falciformis, Aldr.—*M. atlanis*, *M. devastator*, N. America (Aldrich, 1916).

S. (*B.*) *filipjevi*, Rhod.—Larvæ and adults of *L. migratoria*, N. Caucasus (Rhodendorf, 1928).

S. (*B.*) *grylloctona*, Loew.—*Podisma alpina*, Europe (Loew, 1861).

S. haematodes, Meig.—*Chrysochraon dispar*, *Podisma alpina*, Europe (Schiner, 1863).

S. haemorrhoidalis, Meig. (*nurus*, Fall.).—*L. migratoria*, S. Russia (Stepanov, 1882); *S. gregaria*, Algeria (Künckel, under the name *nurus*); *S. paranensis*, Argentina (Lahille, as *nurus*). Records doubtful, as the species normally breeds in excrement.

S. helicis, Towns.—*M. differentialis* and other grasshoppers, N. America (Morgan, 1901; Kelly, 1914; Aldrich, 1916). Hyperparasites: *Aphaereta pilipes*, Say, *Perilampus cyaneus*, Brullé (Morgan, 1901).

S. hunteri, Hough (see also *S. opifera*).—*M. differentialis*, *M. atlanis*, U.S.A. (Hunter, 1899; Morgan, 1901; Aldrich, 1916); grasshoppers, British Columbia (Treherne and Buckell).

S. impar, Aldr.—*Dictyophorus reticulatus*, N. America (Aldrich, 1916).

S. kellyi, Aldr.—*M. differentialis*, *M. atlanis*, *M. femur-rubrum*, *M. bivittatus*, *M. bilituratus*, *M. spretus*, *Chorthophaga viridifasciata*, *Schistocerca americana*, N. America (Kelly, 1914, figures, bionomics); attacking *Dissosteira longipennis*, N. America (Smith, 1915). Hyperparasites: *Brachymeria coloradensis*, Cress., *Aphaereta* sp., *Eupteromalus* sp. (Kelly).

S. lambens, Wied.—*S. paranensis*, Argentina (Lahille, 1907).

S. (*Blaesoxypha*) *lineata*, Fall.—*L. migratoria*, Russia (Rossikov, 1899; Nikolsky, 1911, 1925, etc.); *D. maroccanus*, Sicily (Paoli, 1910), Montenegro (Baranov, 1924, 1925, figures, bionomics); *Calliptamus italicus*, Russia (Moritz, 1915); *Gomphocerus sibiricus*, E. Siberia (Vinokurov, 1927).

S. margareti, Lah.—*S. paranensis*, Argentina (Lahille, 1907).

S. marginata, Aldr.—From dead grasshoppers, N. America (Aldrich, 1916).

S. minuta, Lah., see *Brachycoma acridiorum*.

S. nurus, Rond., see *S. haemorrhoidalis*.

S. opifera, Coq.—*Melanoplus devastator*, *marginatus*, *spretus*, *differentialis*, *plumbeus*, *bivittatus*; *Chorthophaga viridifasciata*, various grasshoppers, N. America (Coquillet, 1892; Kelly, 1914—under the name *hunteri*; Treherne and Buckell; Aldrich, 1916).

S. pachytili, Skuse.—*Chortoicetes terminifera*, Australia (Froggatt, 1910).

S. parvula, Lah.—*S. paranensis*, Argentina (Lahille, 1907).

S. (*Blaesoxypha*) *rossica*, Vill.—*Omocestus haemorrhoidalis*, E. Siberia (Vinonurov, 1927).

S. sarraceniae, see *S. tuberosa*.

S. sinuata, Meig.—*M. differentialis*, N. America (Kelly, 1914; Aldrich).

S. stallengi, Lah.—*S. paranensis*, Argentina (Lahille, 1907).

S. sternodontis, Towns.—*Schistocerca americana*, *Dictyophorus reticulatus* (Aldrich, 1916).

S. striata, F.—*D. maroccanus*, Algeria (Künckel, under the name *atropos*, Meig., see Baer).

S. tuberosa, Pand. var. *sarracenioides*, Aldr.—*M. differentialis*, *Chorthophaga viridifasciata* (Morgan, 1901; Kelly, 1914, as *sarraceniae*; Aldrich, 1916). Hyperparasite: *Brachymeria coloradensis*, Cress. (Kelly).

S. (*Blaesoxypha*) *ungulata*, Pand.—*D. maroccanus*, *Anacridium aegyptium* and other ACRIDIDÆ, Algeria (Künckel, under the name *clathrata*, Meig., see Baer).

Sarcophaga spp.—*L. migratoria*, Russia (Michelson, 1922, bionomics).

Sarcophaga sp.—*Podisma alpina*, Europe (Grassé, 1924, bionomics).

S. (*Blaesoxypha*) sp.—*Oedipoda coerulescens*, *Calliptamus italicus*, Montenegro (Baranov, 1924, 1925).

Sarcophaga sp.—*Bryodema tuberculata*, Russia (Moritz, 1915).

Cynomyia pictifacies (author ?).—*Locustana pardalina*, S. Africa (S. Afr., Central Locust Bureau).

Other Parasitic Flies.—Apart from the SARCOPHAGIDÆ about which, as we have seen, there are at least some preliminary data, some flies of other families have been recorded in the literature as bred from ACRIDIDÆ, living or dead. Some such records obviously refer to cases of the larvæ developing

simply in decaying dead grasshoppers, but there is no doubt that there are true parasites of ACRIDIDÆ amongst at least the family TACHINIDÆ.

List of Tachinidæ parasitic in Acrididæ

Acemyia dentata, Coq.—*Melanoplus differentialis*, U.S.A. (Morgan, 1901); *Xanthippus neglectus*, *Chorthophaga viridifasciata*, British Columbia (Treherne and Buckell).

Acomyia acuticornis, Meig.—*Anacridium aegyptium*, Europe (Ribaga, 1902, under the name *Tachina subrotundata*, Rd., see Baer).

Arrhinomyia innoxia, Meig.—*Acrydium bipunctatum*, Russia (Rodzianko; as *Hypostena setiventris*, Rond., see Baer).

Euphorocera claripennis, Macq.—*M. differentialis*, U.S.A. (Morgan, 1901).

Masicera pachytyli, Oliffe.—*Chortoicetes*, Australia (Oliffe, 1891).

Meigenia floralis, Fall.—*Chorthippus parallelus*, Europe (Kleine, 1909).

Miltogramma duodecimpunctata, Wulp.—*Patanga succincta*, India (Lefroy, 1906; a doubtful record, as members of this genus are parasites on the larvæ of fossorial wasps).

Finally, there are some records of flies of other families. Thus, Sajo (1904) records *Gymnosoma rotundata*, L. (PHASIINÆ), as a parasite of *Dociostaurus maroccanus* in Hungary, but this species is known as a special parasite of Hemiptera, and the record is probably erroneous. Morgan (1901) states that the Muscid, *Lucilia caesar*, L., was bred from *M. differentialis*, but this must be a case of saprophytism, not parasitism. Very remarkable is a record by Sacharov (1914), who bred *Anthomyia* sp. from *L. migratoria*; this record is corroborated by Mr. N. G. Olsufiev (*in litt.*), who found larvæ of a small fly in large numbers (up to 102) inside the locusts, their presence being fatal to the host.*

FIG. 60.—*Eutrombidium locustarum*, Walsh; larva on the wing membrane of a grasshopper (after C. W. Howard).

Red Mites.—The larvæ of the red mites, as external parasites of hoppers and adult ACRIDIDÆ, are well known (Fig. 60). For detailed information, see above, p. 116.

Tracheal Mite.—Quite recently two American entomologists have discovered another interesting parasite of ACRIDIDÆ, to which I should like to draw the special attention of all those interested in the problem because it seems not improbable that parasites of this kind are not uncommon, but have been overlooked. This is the tracheal mite, *Locustacarus trachealis*, Ew., which has been found in the tracheal system of *Hippiscus apiculatus* and *Arphia carinata* (Wehrle and Welch, 1925; Ewing, 1924). This mite belongs to the family TARSONEMIDÆ and is remarkable for the presence of only three pairs

* Nocedo (1918) records as parasites of *Schistocerca paranensis* in Guatemala *Muscina stabulans*, Fall., a new Tachinid, two Phorids, viz. *Aphiochaeta scalaris*, Lw., and *A.* sp., and an Anthomyiid, *Fannia canicularis*, L.

of legs, the fourth (posterior) pair being entirely lacking even in the adult; which resembles in this respect the larvæ of the red mites.

Infestation is sometimes so severe that the air-sacs and larger tracheal tubes in the thorax and the first three abdominal segments are almost completely blocked with mites and their eggs; when a grasshopper so heavily infested is dissected, the mites and eggs show as a yellowish mass through the walls of the sacs and tubes. The segments mentioned are those most often affected, but the infestation may spread into the head and abdomen up to the sixth segment; all the tracheæ may be filled with mites, except those that are too narrow for them. As far as could be ascertained, only the adult grasshoppers are attacked, and in all cases they were females, but this may be due to an insufficient number of observations.

The effect of the parasite on the host was not studied in detail, but it is strikingly similar to the Isle of Wight disease of the Honey Bee, also produced by a tracheal mite (*Acarapis woodi*). The obstruction of the tracheæ and air-sacs must seriously interfere with normal respiration and affect the general activity of the insect. Apart from this, there are some indications that the mites probably obtain nourishment by piercing the walls of the tracheæ and air-sacs and sucking the blood of the host; it is uncertain how seriously this may affect the host, but it was observed that the tissues around the point where a mite is attached are usually discoloured. The authors do not mention the possible rôle of these mites during migrations by interfering with the normal functions of the air-sacs, but this must be another important effect of infestation. Whether these parasites can cause the death of the host is uncertain, but two specimens of grasshoppers found dead in the field contained these mites, and one or two living individuals that died in the laboratory were also found to be infested.

The life-history of the mite appears very simple, because adults of both sexes emerge from the egg, and the parasite is able to pass its whole cycle inside the host. The lack of free living larval stages is balanced by two supplementary embryonic stages, deutovum and tritovum, which correspond to the larva and the nymph of other mites. The important problem of the method of infestation remains unsolved, but it seems probable that the mites can crawl out of the tracheæ and pass to another host.

Parasitic Worms.—The occurrence of parasitic worms inside the body of Acrididæ has been recorded by many authors and nearly always as a curiosity. As a matter of fact, however, these parasites are anything but rare, and special examinations of large numbers of North American grasshoppers have shown that normally from 12 to 25 per cent. of them are infested with roundworms (Cobb, Steiner and Christie, 1923, 1925), while there is one case on record when parasitic worms were responsible for a regular epidemic amongst grasshoppers which greatly reduced their numbers (Glaser and Wilcox, 1918).

The worms parasitising Acrididæ are referred to two groups, Nematodes, of the family Mermithidæ, and Gordiacea. These are very different in their anatomical structure and in their habits, but are superficially very similar in appearance. This fact is responsible for the enormous confusion that obtains in the literature, especially entomological literature, since the authors

reporting the presence of parasites in ACRIDIDÆ have referred them either to MERMITHIDÆ or to Gordiacea without any reasons whatever; there are scarcely more than two cases known, when the parasite has been submitted for determination to a specialist. Almost as worthless are most of the records made by some of the earlier helminthologists who separated the species mainly by hosts and published descriptions that do not even make it possible to refer them to one or the other of these two groups.

Relatively better known are the Nematodes of the family MERMITHIDÆ, which also seem to be much more common as parasites (see specially Hagmeier, 1912; Cobb, Steiner and Christie, 1923).

The parasite, as it is known to entomologists, is a very long and fine thread-like worm, coiled inside the body of its host. This form is not yet adult, and becomes so only after leaving the host (through a hole in its body wall) and burrowing into the soil. Here the worms congregate, at a depth of 3–20 cm., in tightly coiled balls, in which there is usually one female and from one to seven males. The eggs in some species (*Agamermis decaudata*) are laid in the same cells where the worms are, and the number of eggs laid by one female may reach the astonishing average of 5000. Based on this figure and the actual number of groups of worms in the ground, the number of eggs to an acre has been calculated in some cases as half a million (Cobb, Steiner and Christie). In other species, as in the European, *Mermis nigrescens*, and the American, *M. subnigrescens* (Cobb, 1926), the female comes out (usually after rain), climbs a plant, and lays eggs on it. The eggs of these species are remarkable for the large branched appendages on both ends which serve to keep the egg on the plant by entangling it in its hairs (Fig. 61); and only hairy plants (*e.g. Plantago lanceolata*) are selected for oviposition. The number of eggs laid by a female of *M. subnigrescens* is estimated by Cobb as several tens of thousands.

FIG. 61.—Egg of *Mermis subnigrescens*, Cobb (redrawn after Cobb).

Where the eggs are laid in the ground, the young Nematode larvæ, which on hatching are only 4–5 mm. long, reach the surface of the ground, find an Acridid, and burrow into it by means of the special lance-shaped mouth organ; it is, however, only the anterior portion of the body of the worm which enters the host, the greater part (about five-sixths of the whole) being thrown off by breaking at a special knot (*Agamermis decaudata*).

The eggs laid on plants are eaten by Acridids with the plant, and in the stomach the egg-shell, under the influence of the digestive fluid, opens into two halves in the equatorial line, and the minute Nematode larva, about one-third

of a millimetre in length, crawls out. The larva must immediately burrow through the wall of the stomach, as otherwise it would be ejected with the excreta, the whole process of the passage of food through the digestive tract of a grasshopper requiring only a few hours. When a larva reaches the body cavity in one way or another, it begins to grow very rapidly, so that in the few weeks of its parasitic life, the Nematode increases in length enormously. Full-grown Nematodes may reach an extraordinary size, compared with their hosts ; thus, *Mermis longissimus* reaches 44 cm. in length.

The effect of the Nematode on its host is undoubtedly very serious, though the exact physiological inter-relations between them are not known. I have quoted above a case of a serious epidemic amongst grasshoppers, and even if such cases are not common, they prove that the parasite can cause the death of its host. Usually death is observed even if there is only one worm in the host, but it frequently happens that there are two or three of them, while the number may reach forty. Grasshoppers artificially infested by Nematodes die about a week after infestation with 6–8 worms ; females infested with one or two Nematodes fail to develop ovaries, and males also seem to remain immature sexually. Glaser and Wilcox state that the percentage of infestation in the field is larger in females than in males, but this is scarcely probable in all cases, since the chances of both sexes of becoming infested are equal.

The systematics of the Mermithidæ are, as I have said, in an appalling confusion, and the majority of the existing records of Acridid parasites are unreliable in a varying degree. I think, however, that it might facilitate further work if a list of species and references is given.

List of Mermithidæ, parasitic in Acrididæ

Agamermis decaudata, Cobb, Steiner and Christie.—*Melanoplus femur-rubrum* and other grasshoppers, U.S.A. (Cobb, Steiner and Christie, 1923. 1925, bionomics).

Hexamermis sp.—*Schistocerca paranensis*, Mexico (Dampf, 1925)

Mermis acrididarum, Linst.—" *Orthacris* sp., *Stenobothrus* sp.," Madagascar (Linstow, 1897).

M. acridiorum, Weyenb.—*Schistocerca paranensis*, Argentina (Weyenbergh, 1876 ; Bergh, 1898).

M. acuminata, Rud.—*Schistocerca americana*, *Melanoplus spretus*, *Dissosteira carolina* (Riley, 1878).

M. albicans, Sieb.—*Chorthippus biguttulus*, *C. scalaris*, *Gomphocerus rufus*, *Oedipoda germanica*, *Dociostaurus maroccanus*, *Parapleurus alliaceus*, Europe (Siebold, 1853 ; Asmuss, 1858 ; Linstow, 1898 ; Hagmeier, 1912 ; Stefani Perez, 1923) ; *Melanoplus spretus*, *M. differentialis*, *Schistocerca americana*, *Dissosteira carolina*, U.S.A. (Leidy, 1856 ; Riley, 1878 ; Chittenden, 1905 ; Cobb, Steiner and Christie refer American records to *A. decaudata*).

M. elegans, Hagm.—" *Stenobothrus*," Germany (Hagmeier, 1912).

M. ferruginea, Leidy.—*Dissosteira carolina*, *Melanoplus atlanis*, *M. bivittatus*, U.S.A. (Glaser and Wilcox, 1919, bionomics).

M. gomphoceri-elegantis, Dies.—*Chorthippus elegans*, Europe (Diesing, 1851).

M. gomphoceri-viriduli, Dies.—*Omocestus viridulus*, Europe (Diesing, 1851).

M. longissimus, Fedtch.—" Locusts," Turkestan (Fedtchenko, 1874 ; Linstow, 1898).

M. nigrescens, Duj.—*Podisma pedestris*, *Mecostethus grossus*, *Parapleurus alliaceus*, *Chorthippus parallelus*, *C. variabilis*, *C. scalaris*, *C. albomarginatus*, *Myrmeleotettix maculatus*, *Gomphocerus sibiricus*, *Psophus stridulus*, Europe (Asmuss, 1858 ; Linstow, 1892, 1898 ; Hagmeier, 1912).

M. praematura, Linst.—" *Stenobothrus* sp.," Madagascar (Linstow, 1897).

M. spiralis, Baird.—" Grasshopper," Brazil (Baird, 1853).

M. subnigrescens, Cobb.—Various grasshoppers, U.S.A. (Cobb, Steiner and Christie, 1923, under the name *nigrescens ;* Cobb, 1926).

Another group of worms, members of which are reputed to be parasites of ACRIDIDÆ, are the GORDIACEA, or hair-worms. In most records the species *Gordius aquaticus*, L., is mentioned, but this must be regarded as an entirely meaningless name, since the original description by Linné does not permit the recognition of this species, and this induced Camerano in his monograph of the group (1897) to reject it altogether, while he refers all cases of occurrence of GORDIACEA in insects to *G. villoti*, Rosa. Most of the records listed below probably do not refer to GORDIACEA at all, but to MERMITHIDÆ, but it is absolutely impossible to decide this point in most cases.

From the point of view of bionomics, very little is known of the GORDIACEA parasitic in insects in general, and nothing at all on those recorded from ACRIDIDÆ. In other species of *Gordius*, so far as it is known, the first larva is aquatic in its habits and normally infests the larvæ of aquatic insects ; when the latter are eaten by fish or by carnivorous insects, these become infested in their turn. Villot (1891) and also May (1919) believe that such a change of host is not necessary in most species of *Gordius* and that the first larva infests insects, both aquatic and those living near water, only by accident. This view can hardly be accepted, since there are some unquestionable records of species of *Gordius* from insects that do not live near water, and it would be difficult to account for their infestation. It is not impossible that future studies will modify the existing views on the habits and development of GORDIACEA, but so far we cannot do more than state that members of this group may occasionally infest ACRIDIDÆ, though the vast majority of records must be referred to the MERMITHIDÆ.

A list of species known from ACRIDIDÆ may help future investigators.

List of Gordiacea parasitic in Acrididæ

Gordius acridiorum, Weyenb.—*Schistocerca paranensis*, Argentina (Weyenbergh, 1879 ; Conil, 1881).

G. acrydii, Dies.—*Bryodema tuberculata*, Europe (Diesing, 1851).

G. aquaticus, L.—*Arcyptera fusca*, *Omocestus viridulus*, Europe (Siebold, 1855 ; Asmuss, 1858).

G. calliptami-italici, Dies.—*Calliptamus italicus*, Europe (Diesing, 1851).

G. oedypodae-biguttulae, Dies.—*Chorthippus biguttulus*, Europe (Diesing, 1851).

G. oedypodae-coerulescentis, Dies.—*Oedipoda coerulescens*, Europe (Diesing, 1851).

G. oedypodae-migratoriae, Dies.—*Locusta migratoria*, Europe (Diesing, 1851).

G. oedypodae-parallelae, Dies.—*Chorthippus parallelus*, Europe (Diesing, 1851).

G. robustus, Leidy.—" Grasshopper," U.S.A. (Leidy, 1851).

G. villoti, Rosa.—*Omocestus viridulus*, Europe (Camerano, 1897 ; Montgomery, 1907).

To conclude this discussion of the worms parasitic in ACRIDIDÆ I would draw the special attention of entomologists, who may happen to find them, to the fact that it is absolutely useless and even misleading to record them under fancy specific names, as is usually done ; in all cases a determination by a specialist must be obtained. The careful collection of material for systematic studies would be of great value, since the progress of our knowledge of these parasites is barred by the unsatisfactory condition of their classification.*

Intestinal Gregarines.—The presence of Gregarines (Fig. 62) in the digestive tract of ACRIDIDÆ is not uncommon. According to the detailed studies of Watson (1916) on the North American species, and of Bush (1928) in South Africa, hoppers in the early spring are free from Gregarines, but they appear later in the season, and towards the autumn practically every grasshopper is infested, the number in some of them reaching as many as fifty. Infestation occurs through the spores which are always present on the ground, grass, and low herbage, and enter the digestive tract with the food. At first the Gregarine fastens itself to the wall of the stomach by piercing one of the cells with its anterior end ; later it lives free in the intestine near its walls ; here the pairs are formed, pairing resulting in the formation of a cyst, the spores from which are ejected with the excreta. When the infestation is very heavy, Gregarines may be seen in the excreta as oval light-yellowish bodies ; they are particularly numerous in the excreta just after a moult (Künckel, 1899).

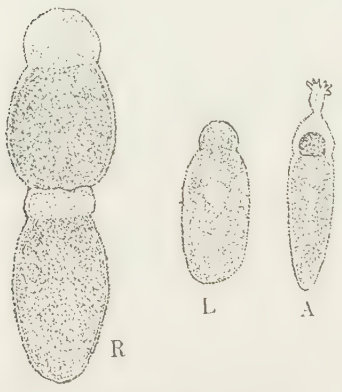

FIG. 62.—Intestinal gregarines of grasshoppers.—R, a pair of *Gregarina rigida*, Hall.—L, *G. locustae*, Lank.—A, *Actinocephalus fimbriatus*, Dies. (after Watson).

The effect of Gregarines on their host is uncertain ; it is not impossible that they are only harmless symbionts, but even in this case they must play some physiological rôle. That they have a local harmful effect is beyond doubt, since the cell pierced by the cephalic end of a Gregarine usually dies, and the feeding of Gregarines on the intestinal contents must occur osmotically, which cannot fail to have some effect on nutrition in a badly infested host, since over a thousand parasites may occur in one individual (Bush, 1928).

The following list is compiled mainly from Watson's work (1916), supplemented by data published by Bush (1928).

* In collecting MERMITHIDÆ it must be remembered that they leave the host when immature and therefore indeterminable ; they must be kept in moist sand until mature, which may happen only after a long time (up to two years).

List of Gregarines parasitic in Acrididæ

Actinocephalus fimbriatus, Dies.—*Dissosteira carolina*, U.S.A. (Diesing, 1859 ; Leidy, 1853, as *Gregarina locustae-carolinae*).

A. amphoriformis, Bush.—Various grasshoppers, Natal (Bush, 1928).

A. giganteus, Bush.—Various grasshoppers, Natal (Bush, 1928).

A. sp.—Grasshoppers, Natal (Bush, 1928).

Gregarina acridiorum, Leger.—*Acrida* sp., *Pamphagus* sp., *Sphingonotus* sp., Algeria and France (Leger, 1893).

G. nigra, Watson.—*Melanoplus femur-rubrum*, *Encoptolophus sordidus*, U.S.A. (Watson, 1916) ; *Cyrtacanthacris ruficornis*, *Lentula* sp., *Zonocerus elegans*, Natal (Bush, 1928).

G. oblonga, Duf.—*Locusta migratoria*, *Psophus stridulus*, Europe (Dufour, 1837 ; Diesing, 1851).

G. paranensis, Kunck.—*Schistocerca paranensis*, Argentina (Künckel, 1899).

G. rigida (Hall), Ellis.—*Melanoplus femoratus*, *luridus*, *femur-rubrum*, *atlanis*, *differentialis*, *coloradensis ?*, *angustipennis*, *Encoptolophus sordidus*, *Hesperotettix pratensis*, *Brachystola magna*, U.S.A. (Hall, 1907 ; Crawley, 1907 ; Ellis, 1913 ; Watson, 1916).

G. locustae, Lank.—*Dissosteira carolina*, U.S.A. (Lankester, 1863).

Gregarinoides locustanae, Fantham.—*Locustana pardalina*, S. Africa (Fantham, 1923, 1924, 1925) ; various grasshoppers, Natal (Bush, 1928).

Legeria sp.—*Phloeonotus jugatus*, Natal (Bush, 1928).

Birds as Enemies of Acrididæ.—I believe that it would serve no useful purpose to enumerate the birds that have been recorded in the literature as enemies of Acrididæ in different countries, and I will only offer some general considerations as to their value in restricting the numbers of these insects.

A correct estimate cannot be obtained by direct observations on birds feeding on Acrididæ ; particularly misleading are reports on the beneficial work of birds as observed during their attacks on swarms of locusts, since in all these observations the superficial impression plays too great a part. Much more reliable in this respect are the results of systematic examinations of the contents of birds' stomachs. Special work of this kind intended exclusively for the valuation of the part played by birds in the regulation of the numbers of grasshoppers has been done once only, by Bryant in North America (1912). His investigations covered two years, one of which was normal with regard to the abundance of grasshoppers, while their numbers were above the average in the next year. Direct observations in the field on the species of birds feeding on grasshoppers and analyses of the stomach contents of various birds led the author to the conclusion that during the years of the mass appearance of grasshoppers species of birds begin to feed on them that do not do so in normal years.

The actual number of grasshoppers devoured during a day by one bird varies, of course, with the species of bird and, partly, with its size ; the latter, however, is of secondary importance, since a heron eats on the average 42 grasshoppers in a day, and a lark—48. Particularly striking becomes the

comparative value of different species of birds, if the whole bird population of the area is taken into account, because certain birds, that do not destroy many grasshoppers individually, may be more abundant than the species feeding on grasshoppers exclusively. Further theoretical computations, such as those given by Bryant, *e.g.* estimation of the number of grasshoppers destroyed by the whole bird population of an area during the whole season, cannot possibly be sufficiently exact; it is clear, however, from all these data, as an undoubted fact, that the normal bird population plays a very important part in the control of the also normal increase in the grasshopper population.

On the contrary, observations on the value of birds during the mass invasions of ACRIDIDÆ, particularly of locusts, do not indicate that birds are normally a great factor in reducing such outbreaks. All these observations are based on single cases of destruction of a band of hoppers, or of a swarm of winged locusts, but the relative number and size of locust bands and swarms, compared with the numbers of birds engaged in destroying them, is in most cases infinitely greater, and their actual economic importance cannot be judged from purely spectacular impressions. It is possible, of course, that in some cases certain birds can play a considerable part in the suppression of an outbreak of locusts, which is already on the decline, and at that period it would be very important since birds not only destroy, but scatter the locust swarms, thus accelerating the process of disappearance of swarming forms.

Thus, we may conclude that the fundamental importance of birds consists in supporting the normal balance of the quantities of grasshoppers, their rôle being particularly great during the years of minimum abundance; as regards locusts, birds play a rôle which is very spectacular but not so effective, though the collateral results from scattering the swarms may be considerable.

Quantitative observations and analyses of the food of birds in grasshopper and locust areas, *especially in the years of minimum*, might supply important new data for a thorough estimation of their activities. Work of this kind is urgently needed in all affected areas.

During these observations, it must not be forgotten that birds destroy the parasites as well as the hosts, and Portchinsky (1894) even suggested that the pink starling (*Pastor roseus*), one of the best known beneficial birds, kills locusts especially to obtain the fly larvæ from them; this suggestion is based on the fact that the starlings kill many more locusts than they can eat. This point could be settled without much difficulty by examinations of the contents of the birds' stomachs in which it is easy to find and count both the mandibles of ACRIDIDÆ and the strongly chitinised mouth hooks of the fly larvæ.

Other Vertebrates.—There are in the literature very numerous records of locusts being eaten during outbreaks by various vertebrates, such as monkeys, lizards, snakes, toads, hedgehogs, foxes, dogs, etc., but it appears that hardly any of these animals play any *constant* part in the control of ACRIDIDÆ, the vast majority taking to feeding on them only when they are too abundant, and the numbers of these animals are relatively too small to have any serious

effect. It is not impossible that certain small Insectivora and rodents include ACRIDIDÆ in their normal diet, but reliable data are lacking on this point.

Carnivorous Insects and Spiders.—Mantids of various species pray on ACRIDIDÆ fairly regularly, and the same can be said of certain larger long-horned grasshoppers (*Saga*, *Decticus*, etc.); these latter, however, are mixed feeders, and during mass appearances, are inclined to become regular pests of crops. Many other carnivorous insects, large enough to overcome such a prey, also feed on ACRIDIDÆ, and so do many spiders, but I refrain from quoting records of this kind, since all these are clearly only accidental enemies, of no regular value in reducing the number of the pest, even during the normal years, while their rôle during outbreaks is quite negligible.

FIG. 63.—*Sphex subfuscatus*, Dahlb., with its prey (after Künckel).

Hunting Wasps.—The attention of many entomologists has been drawn by the hunting wasps of the family SPHEGIDÆ, which attack adult Acridids and their hoppers, paralyse them with their sting, and then carry them to their burrow, where an egg is deposited on the victim. The larva on hatching is thus able to find food, which is not only fresh but alive, though unable to move.

In Europe and neighbouring countries the commonest of these wasps is *Sphex subfuscatus*, Dahlb., a black species with yellowish wings (Fig. 63) that has been recorded many times as attacking the Moroccan locust and other species. Other species of the same genus, as well as of the related genera *Tachysphex* and *Tachytes*, also provision their burrows with ACRIDIDÆ, and the same is known with regard to *Stizus fasciatus*, F., another member of the same

family, but very far removed from the other three genera. A secondary parasite of *Sphex subfuscatus*, the fly *Heteropteina stictica*, Mg., has been recorded ; it lays its eggs on the already paralysed victim (Ferton, 1903).

While the hunting wasps are extremely interesting from the point of view of a biologist and zoo-psychologist, their actual value in control is, of course, very small, and I do not think it worth while to compile all the records of species known as enemies of ACRIDIDÆ in various countries.

Fungous Diseases.—Epidemics amongst ACRIDIDÆ caused by parasitic fungi have often been recorded in the literature, but in the case of one species only is there sufficient information, the data relating to the others being either very incomplete or unreliable.

The only relatively well-known fungus is *Empusa grylli*, Fr., and epidemics caused by it have been recorded amongst North American grasshoppers (*Melanoplus* spp. and other genera), the European *Calliptamus italicus* and a number of other grasshoppers, the South African Red Locust (*Nomadacris septemfasciata*) and some other species. From this may be concluded that this fungus is very widely distributed and infests many hosts, but is nevertheless restricted to certain ones. Indeed, some species are never affected by *E. grylli ;* perhaps the best example is provided by *Locusta migratoria*, which lives in localities where the climatic conditions are perfectly suited to the fungus, but is never attacked by it.

FIG. 64.—Italian locust killed by *Empusa grylli* (redrawn after Uvarov).

The best and most recent work on *Empusa grylli* was published by Skaife (1925), and the following description is based mainly on his paper.

ACRIDIDÆ affected by the fungus can be recognised at once ; they climb to the extreme tops of shrubs and herbaceous plants and die with the head always directed upwards, and the front and middle legs embracing the plant, while the hind legs are usually widely extended sideways (Fig. 64). The majority of infested individuals die during the afternoon, between 3 and 7 p.m.

Approximately an hour after death, there appears on the body of the host a very fine whitish, yellowish, or greenish down, concentrated mainly on the intersegmental membranes of the abdomen, round the neck, at the base of the antennæ, and on the joints of the legs. This down consists of numerous clavate conidiophores (Fig. 65, K) which are placed so densely as to form a brush. At the tip of each conidiophore an oval or pear-shaped conidium, 25–45 microns long, is formed ; it always contains one or two drops of fat. During further development, the stem of the conidiophore begins to swell, apparently because it absorbs water, and presses on the septum separating the conidium from the stem ; finally the conidium separates at the septum and is thrown off with considerable force. This throwing off of the conidia occurs, as a rule, in the evening, when locusts are all densely clustered on plants, and this increases

the chances of a conidium striking an insect to which it adheres owing to part of the viscous contents of the conidiophore flowing out of its broken end. Given favourable weather conditions, a conidium that has stuck to a locust begins to germinate and sends off a fine thread which penetrates the body of the locust.

The conidia, which fail to strike a locust when thrown off, can also germinate under favourable conditions, producing secondary conidia, which are somewhat smaller and more rounded than the primary ones (Fig. 65, BK). The secondary conidia are also thrown off when ripe and probably can infest a locust, though this has not been proved experimentally. It is unknown whether secondary conidia can produce tertiary ones, if necessary.

According to some authors, an infection is possible also through the alimentary canal, but in the experiments of Skaife, who gave locusts water

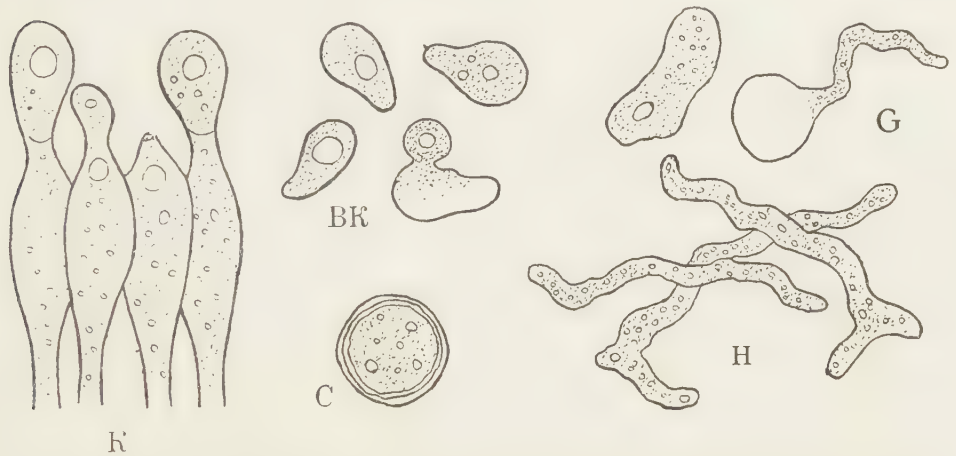

Fig. 65.—Development of *Empusa grylli*.—K, conidia.—BK, secondary conidia.—H, hyphæ.—G, germinating conidiophores.—C, resting spore (after Skaife).

to drink containing a great quantity of conidia, no infection was produced. Since the fungi of this group attack various sucking insects like Aphids, etc., it must be assumed that infection by means of ejected conidia is a normal occurrence.

The conidia retain the power to germinate for about three days only, and after this do not do so even in water. Germination is a very rapid process, so that the chances of a locust's avoiding infection by moulting are very small.

All attempts to cultivate this fungus on artificial media have proved unsuccessful, but germination was observed in the blood of the Brown Locust, though the growth stopped early. It is remarkable that no germination was obtained in the blood of other species of Acrididæ, showing that this fungus has very specialised requirements.

Further development of the fungus inside the body of the locust occurs as follows. The first germination tube which penetrates the body develops septa within it and becomes a hypha ; the hypha forms branches, and on the branches some round bodies are produced which soon become free and are carried by

the blood to other parts of the body of the host. Five or six days after infection these bodies can be found everywhere, though mainly in the abdomen. At this stage the insect dies, and if the weather conditions are favourable, the bodies develop long hyphæ containing drops of fat. These hyphæ are without septa and are scarcely branched (Fig. 65, H) ; they pierce the walls of the locust body and form conidiophores, thus completing the full cycle.

On some locusts, which have died from the fungus, no formation of conidiophores can be observed, and their bodies shrink and dry up. If such specimens are examined, it will be found that they contain a large number of resting spores (Fig. 65, C), which are round, about 30 microns in diameter, and with thick double walls. Formation of resting spores, instead of conidia, is observed particularly during dry weather. What the further fate of these resting spores may be has not been ascertained, as all attempts by Skaife to make them germinate were unsuccessful. Nowakowsky (1882), however, observed their germination, formation of conidiophores, and throwing off of conidia.

It has been stated that the same fungus attacks caterpillars, but Picard (1914) believes that the fungi infecting ACRIDIDÆ and those parasitic on caterpillars belong to different biological species, though practically indistinguishable on morphological characters. Moreover, experiments in infecting one species of Acridid with the fungus from another species have not always proved successful, and this tends to show that there may be, perhaps, distinct biological races of this fungus associated with definite hosts.

Both adults and hoppers are liable to infection, the latter even in the second stage. It is very interesting to note that a certain percentage of locusts seems to be immune against infection ; Skaife kept in one small cage several hundreds of infected locusts, and finally only fifteen survived ; these were kept for two more weeks without showing any sign of infection. Dissection of them disclosed the presence of the round hyphæ, but no further development occurred ; this may be explained either by the individual immunity of certain locusts or by the presence of abnormally weak races of the fungus.

Apart from such exceptional cases, the effect of the infection is invariably fatal, death occurring about five or six days after infection. In the earlier stages there are no outward signs of infection, but a few hours before death the abdomen begins to swell, and the insect climbs a plant. The body of a dead locust is completely filled with hyphæ, and all organs and muscles are destroyed, so that it is difficult to understand how the insect could move at all.

All observations on the fungus show beyond doubt that infection is only possible if the weather is favourable, that is, sufficiently damp and warm. If it is not so, the fungus remains in the stage of resting spores until the next outbreak of infection. Since it is practically impossible to induce the resting spores to germinate, it remains a mystery what the natural conditions are that give rise to a mass infection after several years without an epidemic. Once started, the epidemic spreads with a great rapidity, and large areas may be cleared of locusts within a few days. In this sudden suppression of mass outbreaks lies the great importance of *Empusa grylli*, even though it does not play any part in control under normal conditions.

Of other fungous diseases I might mention *Fusarium* (*Lachnidium*) *acridiorum*, Giard, described from Algeria where it was observed on the adults of *Schistocerca gregaria*. The disease can be recognised by the presence of dark spots on the underside of the abdomen and the sternum. The infected locusts do not die, so that the disease cannot be of great importance. Vinokurov (1927) records that amongst grasshoppers, *Chorthippus albomarginatus*, which died from an epidemic, some proved to be infected with this fungus, while others were not (see also Picard, 1914, where a bibliography is given).

Of considerable interest, owing to their being common and widely spread,

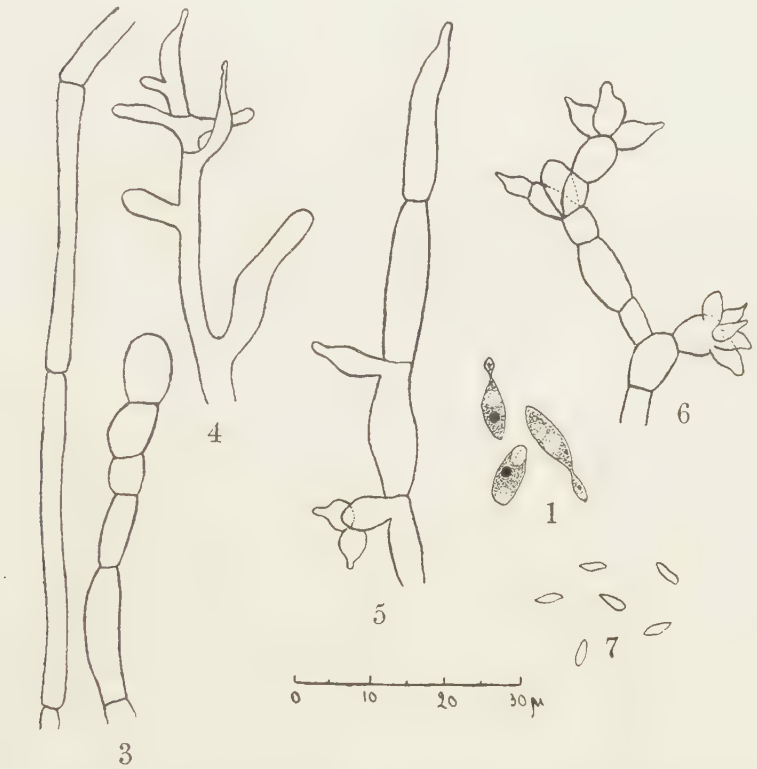

FIG. 66.—*Isaria stenobothri*, Holl. and Mor.—1, yeast-like cells in grasshopper blood.—3-6, mycelium in artificial cultures.—7, spores (after Hollande and Moreau).

are the yeast-like organisms recently discovered in the blood of various ACRIDIDÆ (Fig. 66). Investigations by Hollande and Moreau (1922) have shown that infected ACRIDIDÆ lose the ability to fly and jump with difficulty and very unwillingly; only adults are infested, the organisms being seldom found in hoppers and then in small numbers only. The blood of infected individuals becomes milky and opaque, probably because of the large quantity of proteins present. Microscopic examination reveals that the number of the blood corpuscles in infected insects decreases, because the parasites enveloped by the leucocytes prove to be not only capable of withstanding phagocytosis, but cause the degeneration of these corpuscles. The parasites can also be

found in the fat-body, the cells of which lose their fat and become filled with albuminoid crystals ; the muscle fibres also degenerate under the influence of the parasite, which accounts for the behaviour of the infected insects. Finally, the host dies, death occurring under experimental conditions after five to six days.

On artificial media these yeast-like organisms produce a mycelium with conidia. Hollande and Moreau refer the fungus to the genus *Isaria* (which is mainly a dumping-place for less-known forms), and call it *Isaria stenobothri*, Holl. and Mor., but Grassé (1924) is inclined to think that the fungus is related to the Ascomycetes and belongs to an undescribed genus.

Infection probably occurs through the excreta containing the yeast-like stage, but it is not impossible that there is a conidial stage as well ; in this case infection may be carried by means of spores through the mouth (with food).

In Pospelov's opinion (1926), *Isaria stenobothri* may be, like some other organisms (see below), a normal symbiont of Acrididæ, becoming only occasionally a dangerous parasite.

Bacterial Diseases.—The problem of the bacterial diseases of locusts achieved great popularity from the moment when a French bacteriologist, d'Herelle, announced his discovery of a bacterial epidemic amongst locusts in Yucatan (1911). The extreme optimism of that author, coupled with insufficient technical investigation and combined with his tendency to promise immediate practical results in locust control, led to the appearance of a great mass of literature on the subject. While we may omit for the time being all practical applications of the problem, we must discuss briefly its theoretical side.

It must be stated first of all that the voluminous literature just mentioned concentrated almost entirely on the question of the practical application of the bacillus discovered by d'Herelle, and a scientific study of the organism itself remained in the background. A certain amount of work, however, has been done in that direction, and some information on the bacterial diseases of Acrididæ has accumulated as a result.

Relatively complete data on the natural development of the disease caused by *Coccobacillus acridiorum*, d'Herelle, were communicated by this author himself (1914), but these are far from being exhaustive or exact. The external symptoms of the disease, according to d'Herelle, are identical in the case of locusts in the field and those artificially infected in cages ; in his further accounts, therefore, he never states whether the facts described refer to field observations or to laboratory experiments, and there is a very strong suspicion that the whole description is based on the latter only. It is not impossible, of course, that there is actually no substantial difference between the course of the disease in the field and in the laboratory, but direct evidence in favour of this is lacking, while certain points of d'Herelle's description show that the conditions under which his experimental locusts were kept could not be called normal ; he, for instance, states categorically that it is absolutely impossible to keep locusts alive in cages longer than 15 days.

The symptoms of the disease, as described by d'Herelle, are as follows.

After the incubation period, the length of which depends on the virulence of the bacillus, on the individual resistance of the insect and on the weather conditions, the contents of the stomach become liquid, blackish in colour, and resemble agglutinated blood. The locust ceases to feed, becomes languid, is unable to jump, and seeks refuge under and inside shrubs. After this the contents of the intestine liquefy also, becoming at first yellowish, then darker, until they are almost black ; a light pressure at the abdomen at this stage causes a drop of this liquid to appear from the anus. Then a diarrhœa begins, and the excreta adhere to plants. A few hours later, the insect falls on one side, its jumping legs contract spasmodically, and death occurs in a few minutes or a few hours. After death, the bodies decompose very rapidly, and the outer integument assumes a dark colour. In the contents of the stomach of diseased locusts, enormous numbers of coccobacilli may be observed, so much so that under the microscope the appearance of a pure culture is obtained, and an examination of other parts of the body shows that all the tissues are subject to the attacks of the bacilli. *Coccobacillus acridiorum* itself is described as a highly polymorphic organism, appearing either as a coccus or as a bacillus. I will not give here the bacteriological characters of the organism as described by d'Herelle, but would like to point out that other authors consider them entirely inadequate for an exact determination.

These data practically exhaust the information on the nature of *Coccobacillus acridiorum* published by the author, since the further parts of his main paper (1914), as well as numerous other publications, deal with the technique of practical application of the bacterial method of control. One point, however, is of theoretical interest and may be conveniently discussed here. This is the question of how the epidemic spreads in nature.

d'Herelle stated very definitely, but without describing the respective experiments, that infection takes place through the food, and he believed that in nature it occurs owing to healthy locusts eating plants smeared with the excreta of diseased individuals. Another cause of spread of the disease he found to be due to the cannibal habits of locusts. These habits, according to him, are so widely spread that larger hoppers devour smaller ones whenever they have a chance. His observations, in fact, led him to the remarkable conclusion that "the most powerful enemy of locusts are the locusts themselves." This statement must be regarded as very typical of the ease with which d'Herelle deals with all his problems, and every entomologist will be left in great doubt as to the real importance of occasional cannibalism in the spread of infection.

Transmission of the disease to the next generation occurs during oviposition by such females as are not seriously affected ; the bacilli then get into the egg-pod with the secretion of the accessory glands. Though d'Herelle avoids saying on what ground this statement is based, it seems to be a purely theoretical suggestion.

The results of the epidemic, according to d'Herelle, are such that a whole swarm under optimum conditions can die out completely in eight days, though the disease sometimes spreads more slowly.

I will not dwell here on the examples of very rapid spread of the artificially introduced disease (we will return to them in the chapter on control), but it is interesting to give an outline of the course of the natural epidemic in Yucatan. It began in 1908 when it affected only a few swarms ; during 1909 the number of the infected swarms increased, and in 1910 the epidemic became general ; in 1911 only a few swarms appeared, and they were all infected ; in 1912 all locusts disappeared. Thus, four years were necessary for a complete destruction of locusts ; this is quite a sufficient period for the disappearance of locust swarms from other natural causes, quite independently of any disease, which we will discuss in a later chapter. It may be mentioned that in this case, as usual, d'Herelle does not give any figures of the number of swarms, percentage of infestation, etc., but only bald statements.

In his further work d'Herelle concentrated entirely on the practical side of the problem, apparently assuming that the study of *Coccobacillus acridiorum* was complete and that nothing could be added to our knowledge of it. This, however, proved to be far from being the case. Apart from the innumerable experiments in practical application of *Coccobacillus* made in various countries, some attempts were made to study the organism from the bacteriological point of view. The first result of these studies was that the cultures of *Coccobacillus acridiorum* distributed all over the world were not identical and included several very different organisms (Merezhkovsky, 1913 ; Glaser, 1918). Further, it was found that everywhere in the local ACRIDIDÆ, without any previous infection with the cultures, there is a very rich flora of various bacteria ; thus, in Canada as many as 16 different organisms were isolated from the local grasshoppers, some of them being almost identical with *C. acridiorum*, and many of these proved to be pathogenic if injected, though the infection did not spread by contact or through the food (Du Porte and Vanderleck, 1917).

Merezhkovsky (1925) at the end of his research on the three different original cultures of *C. acridiorum* came to the conclusion that during the repeated injections, which are necessary to increase the virulence of the organism, the original bacillus is always crowded out by the bacteria from the blood of the experimental insects. He believes these bacteria as well as *C. acridiorum* to be normal elements of the blood and not to possess any pathogenic qualities. This conclusion seems to be too categorical and contradictory of the evidence of numerous other authors who observed unquestionable pathogenic effects of *C. acridiorum*, but always under certain conditions. I think, therefore, that the view expressed by Pospelov (1926, 1926*a*) is more acceptable, namely, that the coccobacilli are normal symbionts in the blood and normally play a useful part in the physiology of the host, but under certain conditions (notably at a low temperature and high humidity) they increase in number to such an extent as to become dangerous parasites and produce a disease of the kind observed by d'Herelle.

From this somewhat protracted discussion, only one immediate conclusion can be drawn, namely that our knowledge of the bacterial flora, whether normal or otherwise, of the ACRIDIDÆ is very meagre, and we can only suspect its

great physiological importance, since the problem is only just open for research.

There are a few other cases of what are apparently bacterial diseases of various ACRIDIDÆ recorded in the literature, but practically all of them emanate from entomologists and contain no bacteriological information, so that their nature remains doubtful. The only case studied bacteriologically was recorded by Kufferath (1921), who received locusts (probably *Dociostaurus maroccanus*) from Greece, where there was an epidemic amongst them, and isolated from them several staphylococci, one of which (*Macrococcus acridicida*, Kuff.) proved to be pathogenic when injected and when the food was sprayed with a culture of it. Since it is always possible to diagnose as pathogenic in experiments an organism that is not so in nature, we must accept these data with certain reservations, the more so as Kufferath was prevented from completing his investigations and published only a brief preliminary communication.

CHAPTER VII

PERIODICITY OF MASS OUTBREAKS

While the damage caused by most insect pests is more or less constant, its extent only varying from year to year, this is not so with the Acrididæ. Indeed, there may be no question of any damage from them in a given region during one year, and the very next year a locust invasion may surpass in importance all the other problems of the agricultural life of the country; conversely, a country overrun with locusts for two or three years may just as suddenly become absolutely free from them so that the population forgets them as one forgets a nightmare.

This irregular periodicity of locust outbreaks attracted the attention of students of the problem long ago, and there has been no lack of attempts to explain it.

The first idea of most authors was to discover a definite periodicity, or the existence of definite cycles of years, coinciding with the decrease or increase of locust numbers. Perhaps, the most definite attempt of this kind was made by Krassilschik (1893), who evolved a "law of locust periodicity" according to which *Locusta migratoria* should appear at the mouth of the Donau every twelve years, and in the Caucasus every five or six years. These figures were obtained by simply compiling the records of the past outbreaks, and no attempt was made to analyse the possible causes of the periodicity. Even if we admit that the figures actually represent the history of the past outbreaks quite correctly, and this is very doubtful owing to the unreliability of many old records, it would be very imprudent to deduce from them a "law" that will regulate in some mysterious way all future outbreaks.

Those authors who, using the same historical method, attempt to explain the possible causes of periodicity venture somewhat further. A typical example of this may be seen in a recent paper by Kulagin (1921), who compiled an enormous amount of records of mass outbreaks of locusts in Europe and tried to connect them with Brückner's climatic periods. The conclusions reached were indefinite and negative rather than positive, but they would not be of interest in any case since the method adopted of collecting the records was anything but scientific. Indeed, the records collected referred to "locusts," *i.e.* to Acrididæ of various species and in various countries with widely different climatic and other conditions, and it should be clear that the climate of different countries does not vary simultaneously nor exactly in the same way, while the effects of these fluctuations on different species of Acrididæ cannot be quite the same. The chronological method can give some valuable

data, but only on the condition that it is applied to one species of ACRIDIDÆ and in one definite country with uniform conditions, so that there is a possibility of studying the decrease or increase in numbers of the insects year by year and in connection with the climatic features of each year. As it is, too much valuable time has already been wasted on hunting up data of the " locust " outbreaks in various old chronicles, some of which do not even make clear distinctions between locusts and other insect pests, and it is to be hoped that in future more time will be devoted to actual studies of the problem as it is before our own eyes.

One useful deduction, however, can be made from various chronological compilations, namely, that it is hardly possible to speak of a definite and regular periodicity of mass outbreaks of locusts or of the existence of a definite cycle of years separating one outbreak from another. On the contrary, everything seems to indicate that we should be better justified in speaking not of a regular periodicity, but of *irregular fluctuations* of numbers of a given species in a country. It is not impossible that in future such data on the fluctuations in different countries may be usefully compared and, if there is a coincidence of periods of outbreaks, an explanation will have to be found, but it is perfectly useless and unscientific to try to solve the problem by speculation, rather than by observation.

There can be no doubt that fluctuations in numbers depend, not on mysterious data of " locust " years, but on some tangible peculiarities of these years, and they can be nothing else than the result of the influence of certain natural conditions on the insect organism, either directly or indirectly. This being so, only a thorough, quantitative, ecological study of each species of ACRIDIDÆ in connection with the fluctuation of all ecological conditions from year to year can give a key to an understanding of the factors controlling the outbreaks. We will now discuss some of these factors—most of them are still unknown to us—and try to estimate their probable value in the process. Though the problem appears more simple with regard to non-swarming grasshoppers, I prefer to begin with the locusts, because more is known of their ecology and bionomics generally.

FLUCTUATIONS IN NUMBERS OF LOCUSTS

The history of the locust problem is full of examples of " sudden invasions " of swarms of locusts, and in most cases the explanation is simple, a migration from another region being usually the one offered. Even when this agrees with the facts, the problem of the mass appearance of locusts in that other region still remains, so that it would be futile to look for an explanation of periodicity in that direction. I have had to mention this view, however, because the theory of migrations has been recently advanced by Nikolsky (1925) as not only explaining the periodicity of outbreaks of *Locusta migratoria*, in definite areas, but even as establishing that the periodicity is only an apparent one. According to this author, the fluctuations in the number of locusts within a certain breeding area are due entirely to periodic migrations of swarms from it and to new immigrating swarms from other breeding-grounds. Thus,

the total quantity of locusts in a given country would be always more or less the same, and only the numbers in different breeding-grounds fluctuate. Since this theory does not hold good even for the species on which it is based, it would be unnecessary to enter into its detailed discussion.

Let us consider now what can be the factors controlling the numbers of locusts.

Climatic Fluctuations.—The importance of climatic fluctuations in connection with the periodicity of locust outbreaks has been often pointed out in the literature, and a few examples will suffice.

Filipjev, in his recent survey of outbreaks of ACRIDIDÆ in Russia in 1921–1924 (1926), very definitely attributes the outbreaks of 1920–1921 to the hot and dry weather, pointing out that the same effect was brought about by similar weather in 1891. Still more numerous examples of the influence of hot and dry weather are quoted by Keppen (1870), so that it would be difficult to doubt the general correctness of this statement. At the same time, the question arises as to exactly in what way can dry and hot weather result in a sudden increase of the numbers of locusts.

Keppen attempted to explain it as follows: "If the weather in autumn during pairing and oviposition is mainly favourable, then these processes continue for a long time, and the number of eggs laid is larger than in a cold and damp autumn." This reasoning was not supported by any facts, nor do we know even now whether the number of eggs laid may depend on the weather conditions. Theoretically it may be suggested that a long warm autumn permits the females to make full use of the reserves of eggs in her ovaries, while cold weather stops their development, but this can be studied experimentally in the laboratory, and until this is done, the explanation cannot be accepted.

On the other hand, a suggestion of this kind is apparently not applicable to certain species, such, for example, as the Moroccan locust, in which oviposition takes place early in the summer, and it seems impossible to look for the causes of the termination of oviposition amongst seasonable changes in the weather.

Of course the opposite effect of weather, in stopping an outbreak when it is at its maximum, is easier to understand. An example of such regulating influence of weather was seen in Central Asia in 1917, when enormous masses of eggs of Moroccan locusts had given rise to numberless bands of young hoppers, but these died out in a few days as a result of a severe drought and complete absence of food. Still more important is the influence of unfavourable weather conditions on the development of fungous and other epidemics often resulting in a complete clearing of vast areas from locusts in a very short time.

In any case, it is only the unfavourable direct influence of climatic fluctuations that appears more or less proved (though far from being known in detail), and that can be held responsible in some cases for a termination, or at least a diminution, of an outbreak. The crucial problem of periodicity is, however, in the causes of the *increase* in numbers of locusts, and in this respect no

satisfactory evidence is available. Theoretically it is also very difficult to imagine how the most favourable conditions can result in a sudden enormous increase in the numbers of locusts in a certain area, and it is clear that climatic factors alone are not sufficient for an explanation of periodicity.

Natural Enemies.—The recorded facts of a complete termination of locust outbreaks as a result of the activities of their natural enemies, especially parasites, are very numerous. There is, however, one feature common to all these records ; they all refer to the periods when the outbreak in the locality was already on the wane. This is only natural, since an increase in the numbers of parasites can only occur when the numbers of locusts are already above normal, and the progressive development of parasites is bound to lag behind that of the locusts. Even if we assume that the first process goes on more quickly than the second (and there are no definite data in favour of this), obviously a period of several years would be required for parasites to catch up with the locusts in order that a decrease in the numbers of the latter would begin as a direct result of parasitism.

This means that the rôle of parasites and, to a smaller degree, of predators is restricted to the regulation of the *normal* increase in numbers of locusts, *i.e.* to the maintenance of the normal balance, but once an outbreak begins, the natural enemies can only influence its course very slightly ; their importance becomes very great only towards the end of the outbreak.

An exception to the above described inter-relations of Acrididæ and their natural enemies is presented by the parasitic fungi, since the development of fungous epidemics does not depend on the numbers of Acrididæ, and it can occur during a minimum in their development, while it may also put an end to an outbreak at its maximum. The rôle of fungous diseases, however, is so intimately connected with the weather conditions that they cannot be considered regular controlling factors of the numbers of Acrididæ.

In any case parasites and other natural enemies play only a purely negative part in the periodicity of outbreaks, and an increase in numbers occurs in spite of their activities, which makes the beginning of an outbreak still more difficult to understand.

Thus, neither climatic factors in themselves, nor the activity of natural enemies, can be regarded as sufficient for a satisfactory explanation of the rapid increase in numbers of locusts in their breeding-places at the beginning of an outbreak.

The Theory of Phases of Locusts.—The problem of periodicity in locusts remained in this unsatisfactory condition until quite recently, when I advanced, at first tentatively as a "working hypothesis" (Uvarov, 1921), my theory of phases of locusts, which has now received support and corroboration from practically all workers on the subject ; numerous new facts permit it to be stated definitely that the phases of locusts are *a fact* of great biological significance that supplies a key to the problem of periodicity.

The essential points of the phase theory are as follows :

Various species of gregarious locusts cannot be considered absolutely stable in all their characters, either morphological and biological ; on the

contrary, there are good reasons for regarding each species as exceedingly plastic and liable to fluctuations in all essential characters. These fluctuations have, of course, certain limitations, but in some cases the bounds are so wide that the extreme forms were often recognised as distinct species. These extreme forms represent what I have called the *phases* of the species, one of them being a typical swarming locust in all its biological characteristics, while the other is a typical solitary grasshopper. The amplitude of fluctuation of specific characters in various locusts is not the same, and, therefore, the difference (morphological and biological) between the swarming and the solitary phase may be more or less striking. Even in those species in which the difference between the phases is very great (*Locusta migratoria*), the extreme forms must naturally be connected by a continuous series of intermediate ones, and no definite dividing line can be drawn. The fluctuations of specific characters in the direction of one phase or the other usually occur in a given locality simultaneously in all individuals of the species, and this is connected with the periodicity of outbreaks ; but in order to understand the connection more clearly, we must turn our attention to definite cases that will serve, at the same time, as proofs of the theory.

The first inducement for the erection of this theory arose out of my investigations on *Locusta migratoria* in the Northern Caucasus (1921). At the very outset I was confronted with the problem that had caused many difficulties to many other entomologists before me, *viz.* the inter-relations of two " species " of the genus *Locusta*, namely, *L. migratoria* and *L. danica*. These two forms, if they are studied in typical examples, differ so markedly both in their morphology and coloration that it is impossible not to recognise them as two distinct species. On the other hand, a study of large series of specimens collected in different localities and at different periods always leaves on hand a number of individuals that cannot be definitely identified with either of the two species ; this induced some authors to regard *danica* and *migratoria* as only extreme individual variations of the same species. During my preliminary investigations of the locust in its natural habitat (1911), I was further confronted with the fact that *danica* and *migratoria* differ not only in morphology and coloration, but in their biology as well ; this caused me to suggest that they are actually distinct specifically, and that inability to separate them was due to insufficient knowledge of all their characters. With this idea in mind, I started to look for definite and reliable characters for separation of the two supposed species, but the logic of the facts accumulated during the work forced me to discard this preconceived opinion and to arrive at conclusions entirely different and wholly unexpected.

Careful morphological analysis of the characters separating *danica* and *migratoria* showed that only two of them are sufficiently reliable, and they both lend themselves to a numerical representation. The first of these is the structure of the pronotum, which in the typical *migratoria* is shorter, wider at the shoulders, and with a more definite constriction in the middle, with the hind angle rounded and the median keel low, straight in profile (Fig. 67, C, D) ; in *danica* the pronotum is relatively longer, more compressed laterally, with

the shoulders narrow, the constriction in the middle feeble, hind angle acute and the median keel high, in profile convex (Fig. 67, A, B). These differences find their best expression in figures, if the pronotum is characterised by the ratio of the shoulder width to the length along the median keel, all other characters being directly correlated with these two measurements.

The second character is that the elytra in *migratoria* are relatively longer and the hind femora shorter, while in *danica* the reverse is observed. The numerical expression of this character is quite simple, the ratio between the length of the femur and that of the elytron representing the variation in both of them.

After submitting to measurement several hundreds of specimens of both forms, collected at different times and in different localities, and calculating

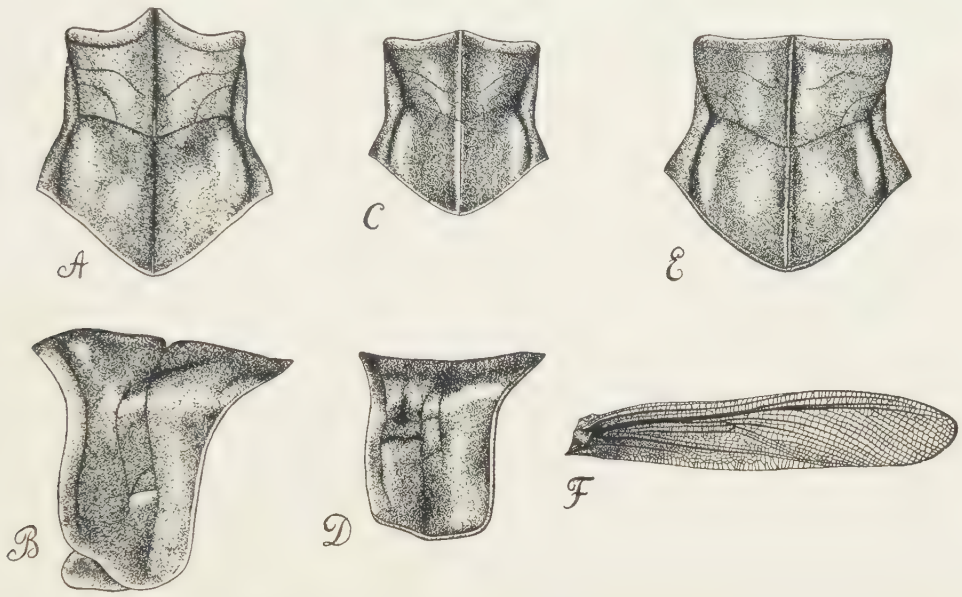

FIG. 67.—Phases of *Locusta migratoria*, L.—A, B, phase *danica*, L, ♀, Turkestan.—C, D, ph. *migratoria*, ♂, progeny of the preceding specimen.—E, ph. *migratoria*, typical ♀, Astrachan.—F, elytron (after Uvarov).

the ratios, I obtained the table (p. 150) which permits some very interesting deductions.

From this table, it may be seen, first of all, that the individual figures for specimens of both forms are highly variable, and owing to this variability there is no interval between a row of the figures for *danica* and that for *migratoria*, which partly overlap each other. This accounts for the fact that the curve representing the variability of pronotal proportion (Fig. 68) in both forms together has only one maximum; the curve seems to indicate that so far as the shape of the pronotum is concerned there is no possibility of regarding *migratoria* and *danica* as two distinct species, or even as two independent forms of the same species. The curve of variability of the femoral proportion (Fig. 69), on the contrary, has two separate maxima, as if the material studied

TABLE SHOWING DIMENSIONS OF DIFFERENT PHASES OF *L. migratoria*, L.

	Number of specimens examined.				Pronotal proportion.				Femoral proportion.			
	Total.	*migratoria*.	*danica*.	Transitional.	Maximum.	Minimum.	Extent of variation.	Average.	Maximum.	Minimum.	Extent of variation.	Average.
1. All *migratoria* ..	171	171	—	—	0·89	0·71	0·18	0·80	0·53	0·40	0·13	0·46
2. All *danica* ..	166	—	166	—	0·85	0·59	0·26	0·72	0·63	0·43	0·20	0·53
3. Palæarctic *danica*	103	—	101	—	0·84	0·59	0·25	0·72	0·63	0·43	0·20	0·52
4. Extra-Palæarctic *danica*	63	—	63	—	0·85	0·66	0·19	0·74	0·60	0·46	0·14	0·55
5. Stavropol province, 1912	25	25	—	—	0·87	0·71	0·16	0·79	0·53	0·42	0·11	0·45
6. Stavropol province, 1913	32	19	8	5	0·87	0·66	0·21	0·77	0·53	0·41	0·12	0·47
7. Valley of r. Kuma, 1913	28	23	4	1	0·87	0·64	0·23	0·78	0·53	0·41	0·12	0·46
8. Valley of r. Kuma, 1914	36	25	8	3	0·87	0·65	0·22	0·76	0·54	0·42	0·12	0·48
9. Lake Vshivoe, 1912	11	10	1	—	0·80	0·74	0·06	0·78	0·48	0·41	0·07	0·45
10. „ „ 1913	8	·2	4	2	0·80	0·69	0·11	0·75	0·51	0·48	0·03	0·49
11. Konstantinovka, Stavropol province, 1911 ..	10	—	6	4	0·77	0·68	0·09	0·72	0·55	0·45	0·10	0·50
12. Kalaus, Stavropol province, 1913 ..	9	7	—	2	0·89	0·73	0·16	0·79	0·49	0·45	0·04	0·47
13. Valley or r. Terek, 1913	26	22	—	4	0·87	0·76	0·11	0·80	0·50	0·42	0·08	0·46
14. Valley of r. Syr-Darya, 1912 ..	16	16	—	—	0·89	0·74	0·15	0·80	0·50	0·40	0·10	0·45
15. Mangyshlak, Caspian Sea, 1911 ..	10	10	—	—	0·87	0·73	0·14	0·80	0·46	0·43	0·03	0·45
16. Korea, 1900 ..	8	—	8	—	0·78	0·68	0·10	0·73	0·60	0·52	0·08	0·55
17. Smyrna	14	—	14	—	0·84	0·67	0·17	0·75	0·63	0·51	0·12	0·55
18. Azores	20	—	20	—	0·85	0·69	0·16	0·75	0·60	0·52	0·12	0·57
19. Congo	9	—	9	—	0·82	0·68	0·14	0·75	0·59	0·50	0·09	0·54
			migratorioides									
20. S.W. Nyasa ..	4	—	—	—	0·94	0·83	0·11	0·86	0·46	0·42	0·04	0·44
21. Lagos	5	—	—	—	0·85	0·78	0·07	0·86	0·46	0·42	0·04	0·44

Relation of shoulder width to the length of pronotum.

could be divided into two distinct groups, whether these are species or units of lower taxonomic value.

The average figures for both forms are also quite distinct and not even close to each other ; the maxima and minima are also characteristic for each form. It may be noted that *danica* is more variable than *migratoria*, and that the *danica* from the Palæarctic region are more variable than the same insect in the tropics.

We will return to an analysis of figures referring to different areas and years later on, but in the meantime we can summarise the results of this attempt at a statistical study of the two forms as rather contradictory and not helping much towards a definite solution of the question whether they are really distinct, or connected by a complete series of transitions in every character.

My attempts to obtain an answer to this question by the study of the male genitalia led to the conclusion that there are no differences in this respect, even between the specimens entirely dissimilar in external appearance. Since,

however, the genitalia of ACRIDIDÆ are very uniform as a rule, I could not attach much importance to this fact.

A comparative study of the coloration and pattern of the adults of both forms showed that no definite colour characters can be given to separate them, both forms being variable in this respect. Generally speaking, however, the extent of variation of colour in *migratoria* is far less than in *danica*, and in the former there is a definite tendency to less defined markings and more uni-

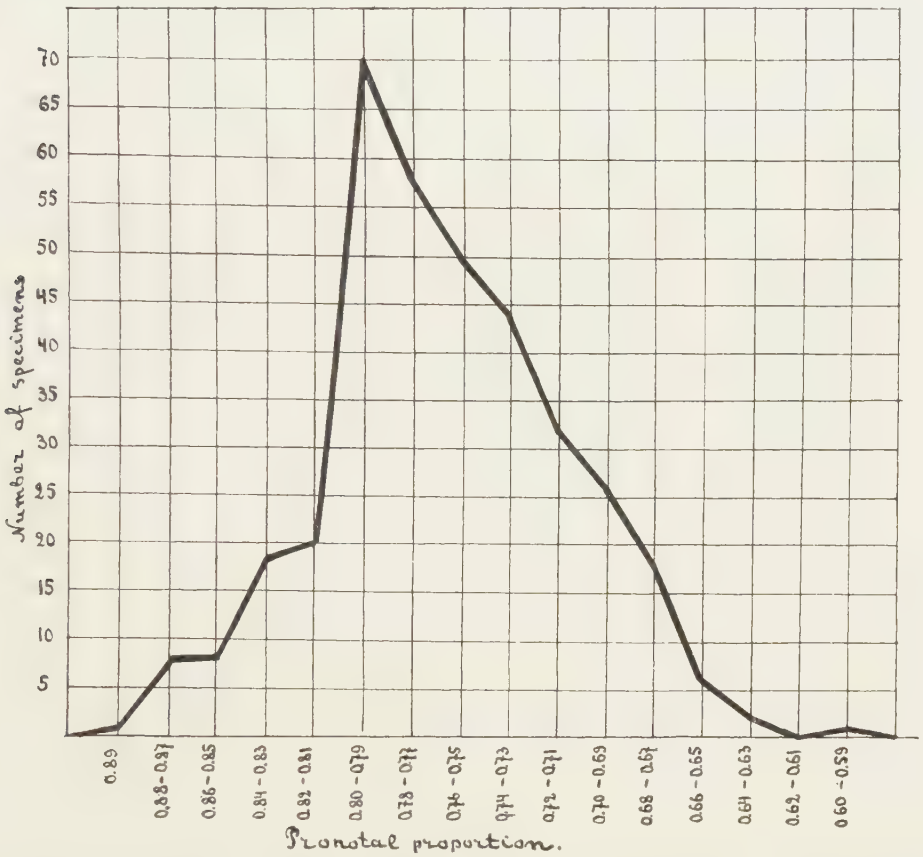

FIG. 68.—Diagram showing range of variation in the pronotal proportion in 358 specimens of *Locusta migratoria*, L. (after Uvarov).

form coloration; especially noteworthy is the fact that the hind tibiæ of *migratoria* are usually yellowish and only red in exceptional cases.

The coloration of *danica* is generally more variable with a prevalence of bright green forms; dark brown, even almost black, forms also occur not infrequently, while the pattern is very variable, but usually well pronounced. The hind tibiæ in *danica* are usually red, but this character is not entirely reliable, as forms typical in other respects may have the hind tibiæ not red.

While the coloration of the adults is thus of very little use for separating the two forms, the coloration of their hoppers is strikingly different, and that not only in some details, but in the whole colour scheme and pattern. In fact,

it is almost impossible to find any definite type of coloration of the hoppers of *danica*, which can be uniformly green, fawn, grey, brown, and even black. Quite the opposite is the case with *migratoria*, in which each larval stage exhibits constant colour characters. Their coloration presents a combination of black and orange-red (or yellow), the earlier stages being almost entirely black, while orange or yellow appears later and extends with each moult without, however, entirely replacing the black. There is of course a certain variability in the coloration of hoppers of *migratoria* as well, but only in the shade of colour, not in the type of pattern ; and the main point is that this type

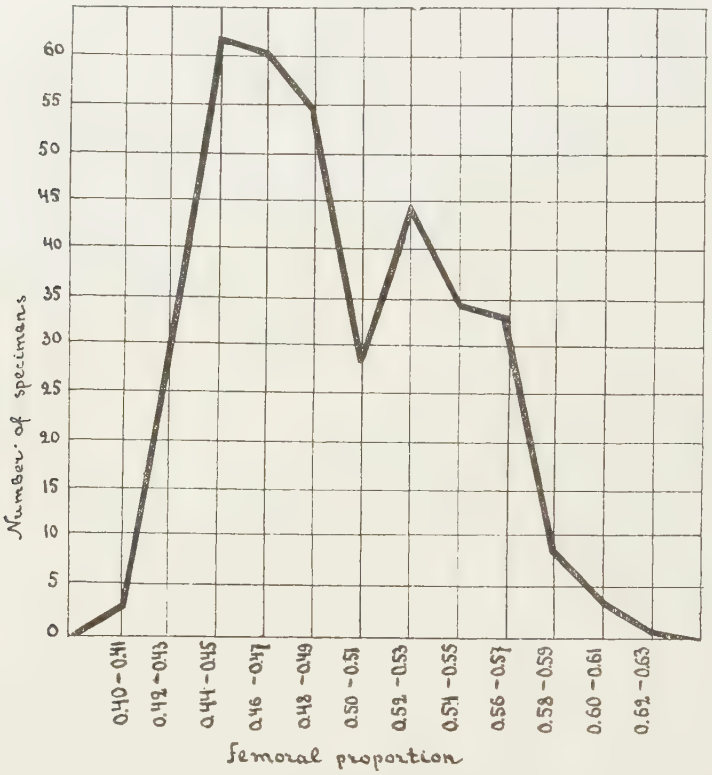

FIG. 69.—Diagram showing range of variation of the femoral proportion in 358 specimens of *Locusta migratoria*, L. (after Uvarov).

of coloration never occurs in hoppers of *danica* in spite of the wide range of variation in the latter. The most important single colour character that separates the hoppers of the two forms is the orange or yellow pigment of *migratoria*, which is never present in *danica*.

A further difference in the two forms is in the degree of sexual dimorphism. In *danica* the adult males are considerably smaller than the females, the average figures of the length of the elytra, body, etc., for males differing from corresponding figures for the females by about 20 per cent. of the latter ; the proportions between parts of the body are, however, constant and not connected with the absolute dimensions. In the *migratoria* there is no apparent

difference in size between the two sexes, and the males on the average are smaller than the females by only some 4 per cent. of the figures for the latter.

A further character connected with sexual dimorphism is observed in the adults of *migratoria* during the period of copulation, when the males assume a bright yellowish general coloration, while the females become more dully coloured. In *danica* no changes in the coloration during the adult life were observed.

The above data exhaust the evidence of the inter-relations of the two forms, as based on their morphology and colour. It is clearly insufficient for drawing definite conclusions with regard to the inter-relations of *migratoria* and *danica*.

When we turn now to the bionomics of the two forms, the differences between them are remarkable. First of all, their ecological requirements are quite distinct, *danica* living almost everywhere, save in deserts and forests, and exhibiting a great ecological plasticity, while *migratoria* is very definitely restricted to a peculiar habitat in the reed-beds of the deltas of rivers discharging into the Black, Caspian, and the Aral seas, and occurs in other conditions only occasionally, though not very rarely (the ecology of *migratoria* will be discussed more fully in the special chapter on the species).

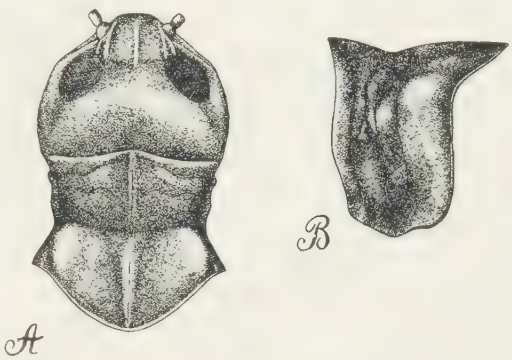

Fig. 70.—*Locusta migratoria*, ph. *migratorioides*, Rch. and Frm., from Lagos.—A, head and pronotum from above.—B, pronotum, side view (after Uvarov).

The most important difference between the two forms is in the behaviour of their hoppers. Those of *migratoria* are typical gregarious insects and comprise dense bands that perform regular mass movements connected with the weather (see Chapter IV), while the hoppers of *danica* do not differ in their behaviour from those of other solitary grasshoppers and do not exhibit any tendency towards gregariousness. The behaviour of the adults is also different in the two forms, one being a typical swarming locust, the other a grasshopper.

A further difference, established by Plotnikov (1915), refers to the development of the embryo, which in *danica* goes on uninterruptedly, while in *migratoria* there is an embryonic diapause (see Chapter II), which it is practically impossible to break.

In spite of all the above data on the differences of the two forms, it still appears impossible to arrive at any definite conclusion as to their inter-relations, and I owe it to a lucky chance that the solution became obvious. This occurred during my work in the Stavropol province of the Northern Caucasus, where in the autumn of 1912 enormous swarms of locusts appeared from the permanent breeding-grounds in the lower reaches of the river Terek. I myself and my assistants collected very large numbers of specimens from the invading swarms, and a study of them showed that they were all most typical

migratoria. Not a single individual resembling *danica* was observed in the field, and we were perfectly convinced that the swarms consisted exclusively of *migratoria* in its most typical form. The figures, which characterise the specimens from these swarms, are given in the fifth line of the table (see p. 150), and they enable us to state that the specimens were remarkably uniform, the extent of their variability (0·16) being less than the average for *migratoria* (0·18 ; see line 1), while the average figures of both proportions are extremely near to the average for all *migratoria*. In their behaviour the insects were typically gregarious.

In accordance with the routine of the control work adopted in Russia, all the swarms were closely watched during their wanderings by the trained staff, and the places where the eggs were laid were marked out and noted on the maps, so that in the following spring we knew definitely that we were dealing with the direct progeny of the swarms. As soon as the hoppers in 1913 attained their third stage, when the colour differences between *danica* and *migratoria* became well pronounced, it became evident that although the bulk of the bands consisted of *migratoria*, there was a considerable admixture of hoppers with the coloration of *danica*, which also exhibited a tendency to desert the bands. A few of the bands reached the adult stage (others were destroyed), and the adults proved to differ considerably from those of their parent swarms (compare lines 5 and 6 of the table, p. 150). Very striking was a considerable admixture of typical *danica*, but still more numerous were specimens of an intermediate character between it and *migratoria*. The bulk of the specimens might have been referred to *migratoria*, but with an obvious tendency to vary in the direction of *danica*. When comparing the proportions of the specimens of 1912 and 1913, one can see that the extent of variation was larger in the second year, the average figures also approaching *danica*. The swarms were less dense than in 1912, and solitary individuals of *danica* were scattered all over the area ; they had obviously deserted the swarms, which gradually dispersed without undertaking any migrations.

Somewhat similar though less striking observations were made on the colonies of locusts at lake Vshivoe (lines 9 and 10) and in the Kuma valley (lines 7 and 8) in two subsequent years.

These observations permit of only one conclusion, namely, that *migratoria* and *danica*, in spite of all their differences, represent only temporary forms of the same species, and we had been actually witnessing the mass transformation of one form into the other. This startling fact required experimental confirmation, which has been supplied by Mr. V. I. Plotnikov, Director of the Turkestan Entomological Station, who was at that time conducting extensive breeding experiments with *Locusta*. His preliminary experiments (Plotnikov, 1915) suggested the possibility of the transformation under laboratory conditions (see Fig. 67, representing the pronotum of a female parent and that of one of its progeny). After an interruption of several years, the experiments were resumed on a larger scale, and the results published (Plotnikov, 1927) entirely corroborated the idea of transformation (though Plotnikov himself, as we shall see later, interprets the results in a somewhat different way). The most

interesting point revealed by the experiments was that the coloration of hoppers of both forms depends entirely on the conditions under which the hoppers are kept, and moreover any individual hopper can change its coloration after a moult, if the conditions are altered. These changes in the coloration of hoppers were found to depend not on temperature, light, and other obvious factors, but only on the degree of density of population in a cage. If for instance 30–50 hoppers were kept in a cage of 450–675 c.cm., they acquired the coloration typical of *migratoria*, no matter whether they were originally of that form or of *danica*. Conversely, about 20 hoppers kept in a cage of 2000 c.cm. appeared unable to retain their original swarming coloration, or remained of the *danica* type, if they were so originally. Of course, these changes occur only after one or more moults under altered conditions. The

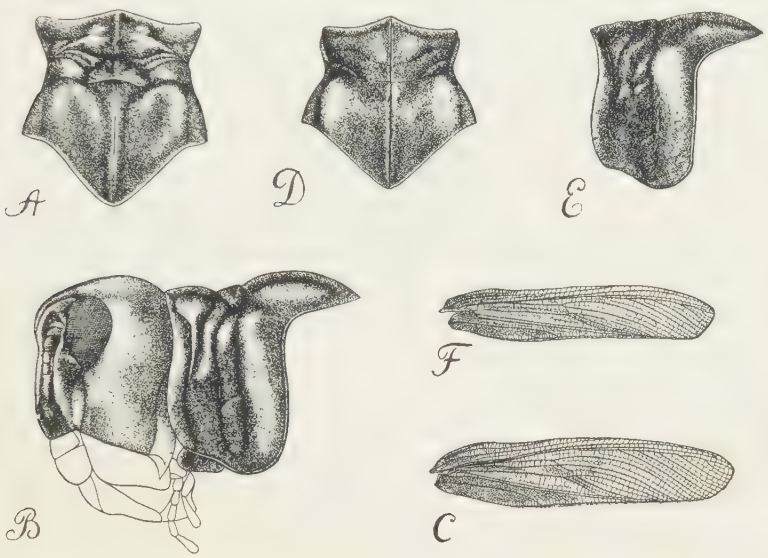

FIG. 71.—Phases of *Locustana pardalina*, Walk.—A, B, C, ph. *pardalina*.—D, E, F, ph. *solitaria*, Uv. (after Uvarov).

density of the hopper population in a cage affected not only their coloration, but even their structural characters : hoppers of the *danica* type, if bred in an overcrowded cage, lost the gibbosity of the pronotal crest, and the adults obtained from them were nearer in the structure of the pronotum to true *migratoria* than to *danica*.

Observations by Plotnikov were further corroborated by the results obtained on several other species of gregarious locusts.

Thus, Faure (1923) working in South Africa on the Brown Locust (*Locustana pardalina*, Walk.) also found two different forms, entirely analogous to the two forms of *Locusta*. The differences of the adults consist (Uvarov, 1921) in the distinct proportions of the pronotum (Fig. 71), and in the ratio femur–elytron ; the male and female of the swarming form are practically equal in size, while there is a strong sexual dimorphism in size in the solitary

form. As regards the coloration of the two forms, the adults of the swarming form are brownish-yellow, while those of the solitary form are often green, but rather variable individually. But the most remarkable parallelism with *Locusta* is observed with regard to the coloration of the hoppers: solitary hoppers are, like *danica*, extremely variable in coloration and often green, while the hoppers of the swarming form might be mistaken for those of *migratoria*, being of the same colour and pattern.

This parallelism between the two species has proved not to be superficial, since breeding experiments by Faure also showed quite conclusively that the coloration of hoppers depends wholly on the density of the population in the cages. It may be observed that Plotnikov and Faure were working practically at the same time and without any knowledge of each other's work.

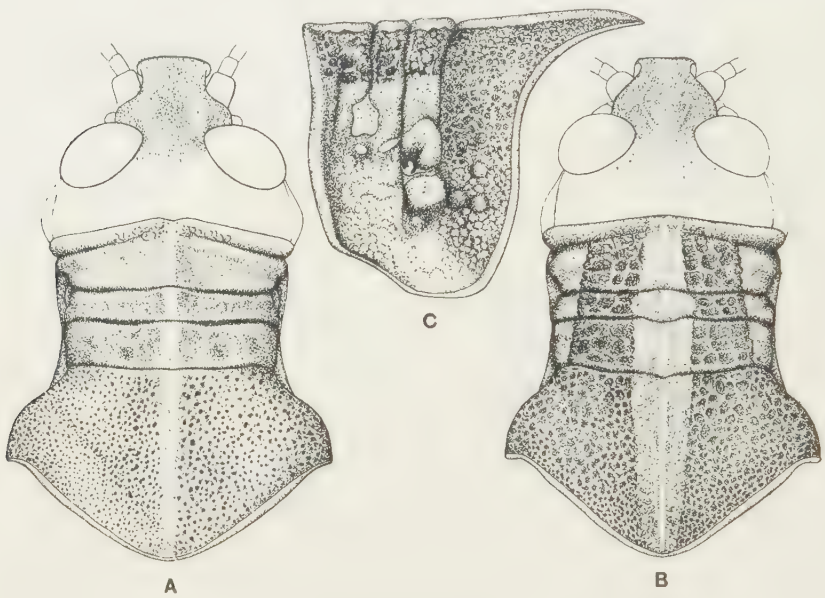

FIG. 72.—Phases of *Schistocerca gregaria* (Forsk.).—A, ph. *gregaria*.—B, C, ph. *flaviventris*, Burm. (after Uvarov).

Field observations by Faure proved also that a transformation of one form into another can also occur under natural conditions. Faure had an opportunity of observing a transformation of the scattered solitary form into dense swarms of the gregarious one, that is, a process the reverse of the one that I observed in the North Caucasus (see p. 154).

Another series of observations refers to still another species of locust (belonging, by the way, to an entirely different subfamily of ACRIDIDÆ), namely, the Desert Locust, *Schistocerca gregaria*. This species also occurs in two forms, one the swarming form well known owing to its destructive habits, and the other, *flaviventris*, Burm., recently redescribed by me (Uvarov, 1923). This last form differs from the swarming one in the more developed crest of the pronotum which is also more distinctly sculptured and has a dark grey pattern (Fig. 72). The general coloration of the adults of *flaviventris*

differs from that of the ordinary form in its greyish tint, without the yellowish that occurs in the swarming form. I was able to establish all these differences only by studying specimens in collections, and I was struck by the obvious parallelism between the two forms of *Schistocerca* and the swarming and solitary forms of *Locusta* and *Locustana*. Since *gregaria* was definitely known as a gregarious form, I ventured to suggest that *flaviventris* may be the corresponding solitary form of the same species, though there was absolutely no information on its bionomics, and I based my suggestion on the assumption that the theory of phases must be applicable to all locusts.

There was, however, not long to wait for the necessary biological evidence on this problem, because Johnston (1926) had an opportunity of making very valuable observations on *Schistocerca gregaria* in the Red Sea province of the Sudan. He records that *flaviventris* occurred there fairly commonly, but always as solitary individuals. After an unusually rainy season, the desert was covered by good grass, and the insects were observed to form fairly dense bands and swarms ; the adults from these swarms were sent to me, and I found them almost typical *gregaria*. There was no doubt that a mass transformation into the swarming form occurred, and my purely theoretical suggestion with regard to the relationship of *gregaria* and *flaviventris* received a definite corroboration. Since the suggestion was based on the theory of phases, the latter enabled me to make a successful prognosis, which is a proof not easily surpassed by any biological theory.

Parallelism between the phenomena observed in *Schistocerca* and the two other species of locusts does not end here. Johnston described the hoppers of the two forms, and a striking analogy exists in that respect also. The hoppers of the swarming form (Plate IX, Figs. 1–5) are yellow with a sharply defined black pattern of constant shape, while the solitary hoppers are wholly green, or with faint traces of black markings (Plate IX, Figs. 1*a*–5*a*). A repetition of breeding experiments gave the same results as with other species, either the swarming or the solitary form being obtainable at will by regulating the density of population. Moreover, the same experiment was repeated, though unintentionally, on a large scale in nature ; when the bands consisting of swarming hoppers were thinned out by poisoned baits, the hoppers in these scattered bands turned into the solitary form, changing their coloration and gregarious habits and dispersing completely.

Johnston points out another character differentiating *gregaria* and *flaviventris* that is only feebly developed in *Locusta ;* the recently moulted adults of the swarming form have a pale pink general coloration that gradually changes to the bright yellow of the sexually mature individuals ; in the solitary form the young adults are greenish, and later they become greyish, but do not change colour on attaining maturity.

The fourth species of locust in which the phenomenon of phases has been established is the South American locust, *Schistocerca paranensis*, Burm. Work on this species has been carried on for several years by Dampf in Mexico. So far, only preliminary results have been published (Dampf, 1925, 1926), but they are sufficient to show that in this case there is the same kind of

inter-relations between the swarming and the solitary form as in all other species. Dampf suggests that the solitary phase of the species is represented by *S. americana*, which was described as a distinct species. The yellow and black coloration of the swarming hoppers of *paranensis* is very similar to that of *peregrina*, while the solitary hoppers are mostly green (Fig. 91). There is some evidence that in this case again the transformation of one form into another depends on the density of population.

Two analogous forms, differing in the structure of the pronotum in the adults (Fig. 92), have been recorded by me in the African Red locust, *Nomadacris septemfasciata*, Serv., and I suggested (1923) that they represent the phases of the species, but there are still very few biological data on this species, which seldom occurs in large swarms.

These five species comprise practically all the larger true locusts of the world (*Patanga succincta* of India and Ceylon swarms very seldom). Of the

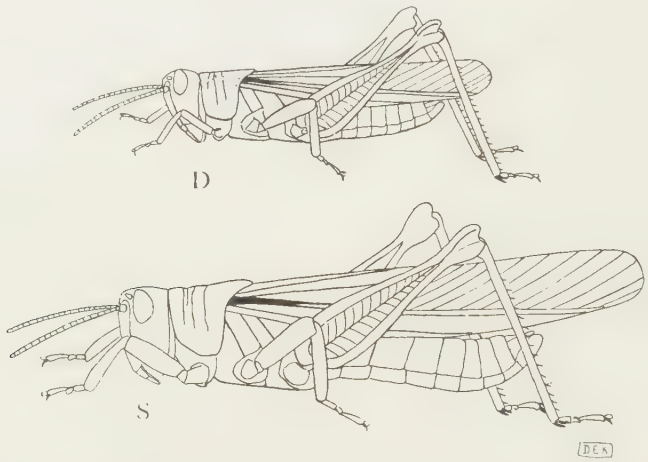

Fig. 73.—Supposed phases of *Dociostaurus maroccanus* (enlarged).—S, swarming.—D, solitary phase (?) *degeneratus*, Bar. (original).

smaller Acrididæ, which swarm more or less regularly, only one species is sufficiently well studied, this being the Moroccan locust (*Dociostaurus maroccanus*). With regard to this species, I have already made the suggestion (1922) that there is a solitary phase of it differing in the adult stage by its shorter elytra and more pronounced pronotal keel. Baranov (1925, 1925*a*) observed in Montenegro a form of the Moroccan locust, which he calls " the pigmy race " and which he describes under the name *degeneratus ;* this seems to be a transition to the solitary form (Fig. 73). The differences of this form from the typical one will be discussed later in the special chapter on the Moroccan locust (p. 231), and here it is sufficient to point out that the solitary individuals of this locust that I had an opportunity of observing in Central Spain in 1926, corresponded very closely with the description of *degeneratus* and represented clearly the solitary phase of the species. There are no data unfortunately on the coloration of hoppers of the solitary form, but those of the

swarming form are remarkably similar in their general scheme of coloration to the hoppers of all other locusts.

The evidence on phases would be incomplete if we omitted the American Rocky Mountain locust (*Melanoplus spretus*). This species caused enormous devastations in the Western United States over a period about fifty years ago, but gradually became less important, and at present the species is regarded as practically extinct in its typical form. However, the members of the U.S. Entomological Commission have already drawn attention to some points bearing directly on our problem. Thus in the First Report of the Commission (p. 245), it is suggested that, after an emigration of swarms of *spretus* from its permanent area, the progeny in the temporary breeding areas may "degenerate" in the direction of *M. atlanis*, which is extremely near to *spretus* in its morphological characters, but is a typical grasshopper, not a locust, in its habits. The hoppers of *spretus* differ from those of *atlanis* in their reddish coloration with clearly defined black pattern, reminiscent of the hoppers of other locusts. The adults of the two "species" differ very little, but the elytra of *spretus* are longer, and its pronotum shorter than those of *atlanis*. This close morphological resemblance and considerable variability of the differentiating characters when studied on a large quantity of material has made some entomologists doubtful of the specific validity of *spretus* and *atlanis* (Somes, 1914). My work on the phases of *Locusta* induced Parker (1925) and Hebard (1925) to suggest definitely that *spretus* is only the swarming phase of *atlanis*; personally I am convinced that it is so, and it would be of the greatest interest to make experiments in breeding hoppers of *atlanis* under conditions of overcrowding. It is a very significant fact that *spretus* is now extinct in nature, which implies that some conditions necessary for transformation are lacking, but I fully agree with Hebard (*l.c.*), who says that there is no guarantee against the return of these conditions and of *spretus*. It is, therefore, to be regretted that the problem is not taken up for study by American entomologists; in any case, such a study would be an immensely valuable contribution to our general knowledge of the phases in locusts.

The Phases and Periodicity.—If the facts concerning *Locusta* and *Locustana* were sufficient for the advancement of the "working hypothesis" of phases (Uvarov, 1921), now, when there is much supplementary evidence on the same two species and several others, it is quite possible to offer a definite phase theory of periodicity of the mass appearances of locusts.

The main starting-point of the theory is that all gregarious Acrididæ, or true locusts, belong to *polymorphic species*, that is, such as are not constant in all their characters, but are capable of producing a series of forms, differing from each other not only morphologically, but also biologically. This series is continuous, *i.e.* the extreme forms are connected by the intermediate ones, but these extreme forms are often so strikingly distinct that they have been taken for different species. These extreme forms I have proposed to call the *phases* of the species, one of them being, by its habits, a typical locust, while the other is an equally typical solitary grasshopper. The amplitude of variation of specific characters may be different in different species, and

accordingly the characters morphological and biological separating the swarming phase from the solitary one may be either very definite, or less so ; an example of the first case is provided by *Locusta migratoria*, of the second by the Moroccan locust.

The variation of specific characters in the direction of one phase or the other usually occurs in the majority of individuals of the species in a certain locality at the same time, so that the species as a whole may be presented as a system in unstable equilibrium. The phases therefore are the temporary conditions of a polymorphic species, and the term adopted for them aims at conveying this idea.

The swarming phase, generally speaking, is characterised by the following principal features : the eggs develop with a diapause ; the hoppers are coloured reddish, orange, or yellow, with well-defined black markings, and are inclined to form bands and wander ; the adults are constant in their morphological and colour characters (the latter, however, undergoing changes in connection with sexual maturation), form dense swarms, and do not develop the sexual products without a migratory flight, owing to an imaginal diapause.

The solitary phase may be characterised as follows : the eggs can develop without a diapause ; the hoppers are variable in colour, and, as a rule, their colour corresponds to that of their surroundings ; they do not form bands and do not wander in masses ; the adults are variable in their morphological and colour characters (but do not change colour in connection with the maturation of the genital products), do not form swarms, and develop sexually without a diapause or a migratory flight.

These diagnoses refer, of course, to the typical cases of the phases, but not to the intermediate forms, in which either one or other character or several of them may be less developed or lacking. I am forced to make this rather obvious remark, because some of the criticisms of the phase theory (we will discuss them later on) were due to the inability of the critics to realise that the phase is only a temporary and often incomplete variation of the species.

The connection between the phases of locusts and the periodicity of their mass outbreaks lies in the fact that it is only because of these phases that the usual extremely rapid increase in the numbers of locusts in a locality, and its equally rapid decrease afterwards, becomes possible.

The course of the phenomenon, very diagrammatically, may be described as follows : A season, exceptionally favourable to the species (or unfavourable to its most important enemies), results in an increase in the number of individuals in a given locality ; in the ordinary solitary grasshoppers, not able to form a swarming phase, a further increase in numbers may follow only if the conditions still remain very favourable, and if they are not, the numbers of the insects return to normal, but in the polymorphic locusts the initial increase in numbers is a factor that releases and directs the mechanism of the formation of the swarming phase. As we now know, this phase develops as a result of the crowding of a large number of individuals in a limited space, and this is exactly what takes place when the numbers of insects increase owing to favourable breeding conditions. Once the development of the

swarming phase has begun as a result of crowding, this process can only increase in intensity, and not decrease, no matter what the other conditions are (apart from the exceptional cases of epidemics, etc.), because the bands of hoppers, once formed, unavoidably grow during their wanderings owing to fusion with other bands. The mass movements of hoppers cannot be without influence on the whole physiology of the insects. I am inclined to suggest that this energetic movement is both the direct result of gregariousness and its cause. I think it possible, for instance, that the appearance of the black pigment in the coloration of the hoppers may depend on the increased chemical changes due to movement, the pigment being probably an oxidation product ; on the other hand, we know that the black colour must increase the susceptibility of hoppers to temperature and result in movement. Thus a vicious circle is formed, and the species involved in it must progress in the direction of further development of the swarming phase. Of course, this theory is easily vulnerable on one point, since the connection between the black pigment and the increase of metabolic changes during movement remains to be proved ; this can be done only by detailed studies of bio-chemical processes in connection with movement. This point, though very important, forms only a part of the problem, while the main issue—that an initial increase in the numbers of individuals can and even must result in the formation of the swarming phase—cannot be disputed in face of the experiments described on previous pages.

In this way it can be realised how the ability to form a swarming phase must result in the increase in numbers of a locust in a progression that would be impossible for grasshoppers not forming phases. It is obvious that the rate of increase may be different and to a certain extent regulated by the climatic and other conditions. As a rule it is impossible to expect the quantity of locusts to increase as early as the first year to the extent of formation of large migrating swarms, but small swarms of adults segregate in the first year, and the gregarious habits during oviposition ensure still more intensive development of the swarming phase in the following one.

The behaviour of swarms depends to a great extent on their size ; in the chapter on behaviour I have pointed out that only sufficiently large swarms emigrate. Very important must also be the degree of development of the genital products, which in the swarming phase requires flight for its accomplishment ; the retardation in the development of the genital products in this phase may be connected with the peculiar conditions of metabolism in the constantly moving hoppers.

A mass emigration from the normal breeding-grounds means a locust invasion into areas that are usually free from these pests ; as a rule only such years of migration and of the appearance of swarms in unusual regions are recorded as the years of appearance of locusts, and they serve to calculate the periodicity.

The fate of the species in the new places where the emigrating swarms oviposit may be different, but the difference is only quantitative—in the sense of a more or less rapid course of the process of transformation into the solitary phase. An impulse to the beginning of this process may be provided by

oviposition in abnormal conditions which causes a reduction of progeny ; a certain part is also due to parasites, the numbers of which increase by this time and the most important of which (larviparous flies and red mites) are transported by the locusts to the new places ; predacious enemies, particularly birds, also often reduce the numbers of locusts considerably. Birds are particularly important at this stage, not because they destroy many locusts, but because they scatter the swarms and thus speed up the process of transformation into the solitary phase. Once an evolution of the species in the direction of the solitary phase begins, the result is a rapid, and often complete, disappearance of locusts as such.

Sometimes the process of the desintegration of swarms is less rapid and happens, not in the first generation, but after two or three of them. This occurs in those cases when the swarms that have emigrated lay their eggs under conditions entirely favourable to the species, *i.e.* similar to those of the permanent breeding areas ; in this way temporary breeding grounds are formed. However, direct observations on *Locusta migratoria* show, that even in these cases the process of transformation is only retarded, and that its direction is determined already from the moment of emigration, which in any case marks the crest of the development of the swarming phase and is followed by the beginning of the evolution towards the solitary phase. This apparently predestined return to the solitary phase after the maximum development of the swarming phase is not easy to explain by the usual factors, and a special suggestion as to its cause can be made, but we will return to it somewhat later.

Such is the course of the process of periodic fluctuations in numbers of locusts in connection with their phases. This is, however, only a theoretical and most typical case, while in practice the cases less definitely outlined and complicated by various collateral phenomena are more common.

First of all, it is necessary to take into account the meteorological conditions not only of various years, but also those connected with the geographical position of the area in question. An example of this kind is provided by *Locusta migratoria*, which has *migratoria* as its swarming phase in the conditions of the south-east of the Palæarctic region, while in the tropics the swarming *migratorioides* phase is still more distinct from the solitary phase (see the table of measurements on p. 150, Fig. 70, and the special chapter on *L. migratoria*) ; on the other hand, in the more northern areas (Central Russia), where the solitary phase is represented by the same *danica*, the swarming phase is much less distinct from it than *migratoria*, *i.e.* the amplitude of variation of specific characters is there much smaller. Accordingly, the phenomenon of phases, so obvious in warmer climates, is much less definite under more northern conditions, where it is easy to arrive at incorrect conclusions owing to the slightness of morphological and biological differences between the phases.

Again, the regularity of the process of the transformation into the swarming phase may be sometimes destroyed by the interference of man, who scatters the bands of hoppers and the swarms when they are just formed, and this stops or, at least, retards the process. In some cases such interference is regular, consisting in artificial changes of the ecological conditions in the permanent

breeding-grounds so that even the initial increase in numbers of the insects becomes difficult. This is what has happened with *Locusta migratoria*, many breeding-grounds of which have ceased to function as a result of the interference of man ; the same is, probably, the cause of the disappearance of the swarming phase of the Rocky Mountain Locust, though it cannot be stated definitely.

To sum up, I believe that the first impulse to the increase in numbers of locusts is given by favourable meteorological conditions in one or several successive seasons, while in the reverse process a considerable rôle is played by the natural enemies, which affect the density of swarms. But the latter process might also be accounted for, at least in part, in a somewhat different way. It may be assumed that the life of the species does not always go on evenly ; there are periods in it when the species, so to speak, accumulates its life energy, which is expressed in the general increase of the vigour of its physiological activities ; favourable external conditions may help this energy to find its expression in increased propagation, which is automatically followed by evolution towards the swarming phase ; then a crisis is reached, the energy of the species begins to decrease, and this inevitably leads to the formation of the solitary phase. From this point of view (I do not insist on its correctness), the phenomenon of phases might be connected with the idea, often expressed in biological literature, of the periodic fluctuations in the energy of the specific life of insects ; the fluctuations in the case of locusts are only accentuated by the phases.

Of course, there is much that remains obscure in the theory of phases, still more that has been only roughly sketched, and all details require deep and thorough study, but the theory has, at least, one advantage—it directs research into a definite channel instead of groping in the dark in the hope of stumbling by accident on the solution of the problem of periodicity.

Criticism of the Phase Theory.—The theory of phases, first published by me in 1921 in a very cautious form and without much detail, found on the whole a sympathetic reception from all entomologists working on the locust problem. However, my aim in publishing it then in its very incomplete form was not to make it known to the world as soon as possible, but was due to a sincere desire for criticism that would be useful in pointing out its defects. I must confess that I was rather disappointed in that respect, the critics being few in number and their remarks mostly referring to details, without touching the main issue. I nevertheless find it necessary to give here briefly the views of my opponents and my remarks on them.

The first to discuss the phase theory was our best student of the Migratory Locust, V. V. Nikolsky (1923). He agrees with me that it is impossible to recognise *migratoria* and *danica* as two distinct species, but he regards the transformation of one into another as not proven. He thinks that our observations on the transformation in nature in the Stavropol province (see above) were not convincing, since no complete transformation of the whole swarms of *migratoria* into *danica* was observed ; this is perfectly true, and I have never stated that this occurred. However, we did observe a striking illustration of the beginning of such transformation, while a certain percentage of individuals

were actually transformed into typical *danica*, which was completely absent from the parental swarms. This observation proved the *possibility* of transformation, which is quite sufficient for the purpose.

Nikolsky has raised a similar objection to the results of breeding experiments by Plotnikov, recorded in my first paper (1921); he pointed out that only in one case did Plotnikov obtain *danica* as the direct progeny of *migratoria*. In my opinion, even an isolated fact of this kind would be sufficient evidence of the *possibility* of transformation.

The main flaw in Nikolsky's criticism is that he demands a direct proof of a mass transformation and is not satisfied with partial evidence of the possibility of transformation; from the point of view of the phase theory, all that matters is the proof that the transformation can occur, though it is connected with an exceedingly complicated assortment of conditions, both physiological and environmental. This point of view was not appreciated by Nikolsky and by some other critics, who seem to assume that the phase theory insists on a magical complete transformation of one phase into another and in the very next generation. In actual fact the theory is based only on the possibility of transformation, and every individual fact proving this possibility weighs heavily in favour of the theory, the more so that there is still nothing to weigh against it, no attempt having been made to suggest another theory of periodicity equally well supported by facts. Nikolsky, it is true, in another paper (1925), in which he hardly mentions the theory of phases, expressed an opinion that there is perhaps no true periodicity, but only migrations of swarms from one breeding-ground to another, but we have already discussed this suggestion (see p. 145).

All the arguments of Nikolsky are entirely overthrown by himself in the appendix to his book (1925), where he gives a translation of the paper by Faure, discusses Plotnikov's experiments, and acclaims the phase theory as a "discovery," overcoming his own scepticism much more easily than I should be willing to do myself.

I have discussed the criticisms by Nikolsky at some length, since they have been repeated by other critics in more or less the same form. Thus Makalowskaja (1925), on the ground of biometric studies on *Locusta* in the Tartar republic (late province of Kazan, on the Volga), came to the conclusion that no transformation took place there and that consequently the phase theory was not corroborated. The absence of phases in the material studied by Makalowskaja would be not unnatural, but as a matter of fact the author simply overestimated the statements of the theory, which does not require a transformation at every time and in every place. Moreover, the conclusions of Makalowskaja are based mainly on measurements of the pronotum, which, as we know (see p. 149), is not a reliable character for phases. But even with the same material, Alpatov (1927) and Gause (1928), who analysed the figures of Makalowskaja more exactly, obtained results that show that the average proportions of insects taken in two subsequent years were different and that an incipient transformation was clearly indicated by them. The differences were slight, but this is due to the fact that Makalowskaja dealt with the locust under the conditions

near its northern climatic limit, where even extreme phases are not strikingly different.

Quite recently Plotnikov has published a pamphlet (1927), in which he summarises the results of his several years' experimental work on *Locusta* as evidence against the phase theory. Since the facts recorded by him, as well as his theoretical conclusions, are of considerable interest, I feel it necessary to discuss his criticism in more detail.

Long series of breeding experiments convinced Plotnikov that the main, and apparently the only, factor affecting the colour and morphology of hoppers and the resultant adults is the density of population in the cages. The influence of crowding, or of isolation, is equally evident in the case of progeny of true *migratoria*, and of true *danica*. Observations on *migratoria* in nature also proved that members of dispersed swarms change their coloration and morphological characters in the direction of *danica*. Recognising thus the existence of two extreme forms of variation in *migratoria*, he proposes to call them ab. *dispersa* and ab. *accumulata*, disregarding, by the way, the usual rules of nomenclature and giving new names to forms already named. As regards *danica*, Plotnikov states that it is able to produce a special form, due to crowding, only under artificial conditions, while in nature it "lives only solitary and gives rise to no aberrations." This statement is not supported by any facts, but it clearly contradicts the evidence obtained in the breeding experiments in which both *danica* and *migratoria* proved to be equally plastic.

A biometrical analysis of mass material on both *migratoria* and *danica* leads Plotnikov to the conclusion that, though the figures overlap, the two forms can be considered distinct. This conclusion is not new (see p. 150), and it does not prove that *migratoria* and *danica* are really two *independent* forms, as has been pointed out by Gause (1928) after very exhaustive biometrical analysis of Plotnikov's own figures.

The only absolute character which, according to Plotnikov, serves to separate them, is that in *migratoria*, even in the ab. *dispersa*, the eggs develop with a diapause, while in *danica*, even when bred in dense cultures, the eggs develop without a diapause. The unreliability of this character is evidenced by Plotnikov himself, who describes exceptional cases, when *danica* developed with a diapause, and *migratoria* without one; though these cases were very rare in a very long series of experiments, still they do prove that this cannot be a character on which to base a permanent distinction between *migratoria* and *danica*.

The crucial point of Plotnikov's paper is his view on the individuals that appear in the swarms of *migratoria*, especially after an emigration and that are indistinguishable in their characters from *danica*. From my point of view, these individuals prove a transformation of one phase into another, but Plotnikov maintains that they are only hybrids between true *migratoria* and true *danica*, which latter was present in the same places. This conclusion of his is based on the fact that he obtained similar forms by crossing *migratoria* and *danica* in cages. Such hybrids he calls "danicoids," and they differ from the

true *danica* only in the less pronounced sexual dimorphism in size (which is one of the characters of *danica*, see p. 152).

Thus, Plotnikov's new theory may be briefly summarised as follows: There are two, extremely close, but independent, forms, *migratoria* and *danica*, which can hybridise, but cannot transform one into another; they "may be regarded, as races, similar to human races, *e.g.* Caucasian and Negro, which also can produce hybrids, but not transform into each other." Both races are able, under artificial conditions, to give aberrations of accumulation and of dispersion; the aberrations produced by different races may be practically indistinguishable on external characters but they always (this is not true, see above) differ by the presence or absence of the embryonic diapause. Further complication is introduced by hybridisation, which also produces forms distinguishable from the aberrations or from the opposite race only by their history, but not by morphological or any other characters.

A very important fact of the absolute parallelism in variation in other gregarious species, Plotnikov dismisses with the remark that this must be explained as a case of homologous variation, a phenomenon widely known in nature. I have never claimed the phase theory to be an exception to all biological laws, and the reference to the theory of homologous variations as covering the phase theory is nothing more than a very strong argument in favour of the latter.

Without discussing Plotnikov's criticism in all details, I would like only to draw attention to its main points. There is no doubt that the author supplies very valuable fresh material in support of the influence of aggregation and dispersion on the coloration and morphology of locusts. The difference between my point of view and that of Plotnikov is that I believe in the possibility of variation, induced by that factor, to go as far as the other phase, as I call it; Plotnikov maintains that the forms produced may resemble the opposite race (as he calls it), but are not identical with it; the forms which are clearly intermediate, Plotnikov explains by hybridisation, though the hybrids do not differ from the varietal forms in anything but their history.

The question arises whether these exceedingly complicated and partly unfounded suggestions make the whole phenomenon any easier to understand, or whether they are nearer the truth. It does not seem so to me, though I have never concealed either from myself or from others that the phase theory, in its present form, is nothing but a crude scheme, and further detailed work will make it much more complicated. Indeed, one of the chief merits of the theory is that it emphasises the extreme complexity of the problem of periodicity and points out the impossibility of settling the latter without a long research in widely varying branches of biology. In these investigations one thing, however, is essential, and that is a clear main idea, not obscured by side issues or by premature conclusions unsupported by facts.

On the whole Plotnikov's paper is to be welcomed for the valuable facts it contains, not for its conclusions, which seem to be dictated not by facts, but by the desire to go far beyond them. Moreover, it must be mentioned that, even if the author were right in his conclusion as to *migratoria* and *danica* being

independent " races," this would not affect the phase theory. Indeed, his own experiments laid such a solid foundation for the theory by proving the importance of the density of population that even his desertion cannot alter their value. If we admit even the correctness of his latest views, this also does not affect the theory very seriously, since it is now based not on one species, but on all locusts sufficiently studied in this respect. There is no doubt that the main idea is sound, and we must only concentrate on the elucidation of details.

Further Work on Phases.—The phases are a particular case of variability of organisms. It is necessary, therefore, to study most thoroughly the variability of each separate morphological and biological character both in connection with the external conditions and independently of them. These studies must be analytical, that is, each character should be studied separately, but it is equally important to study the interaction of characters and the simultaneous variation of groups of characters. In these studies the possible influence of heredity must not be left out of consideration, but, on the other hand, any one undertaking work in that direction must be very careful not to mistake variation induced during the individual development for inherited characters.

The study of variability must be undertaken not only in the laboratory, but also in the field, where it would be possible to calculate the general trend of variation during a series of successive generations. In the field work, the biometric method will be of great value, but it must be never forgotten that the main and principal difference between the phases lies in their bionomics, while their morphology is only the apparent result of some deep physiological differences. A parallel study of the physiology, development, and behaviour of individuals of different phases, again both in laboratory and in the field, is, therefore, urgently needed.

I sincerely hope that the present chapter has shown what interesting biological problems of general importance are raised by the study of locusts. Many of then require both knowledge and equipment not usually to be found in applied entomological institutions, and it would be of the greatest value if some of the investigations were undertaken by university laboratories, which would here find an inexhaustible supply of problems of general interest to work on.

Fluctuations in Numbers of Grasshoppers

The facts of the periodic mass appearance of solitary grasshoppers are well known, as is the case with the true locusts, but the causes of this phenomenon are practically unstudied.

There have been, so far as I know, no attempts to establish a definite periodicity of mass outbreaks of any grasshoppers, but a brief survey of the years of appearance, for instance, of the Siberian grasshoppers, shows conclusively that no regular cycles of periodicity can be discovered. This means that the only hope of finding the actual causes of mass outbreaks lies in detailed studies of the natural balance between the numbers of grasshoppers and their enemies in connection with the fluctuations of ecological conditions.

A very characteristic feature of the outbreaks of grasshoppers is the gradual increase in their numbers, as opposed to the sudden mass appearances of locusts. The reason for this must be the absence of the gregarious phase, which, being itself a result of the initial increase in numbers of the insects, represents, at the same time, a most powerful factor in the further development of the outbreak. Similarly, the decrease in numbers, after the outbreak, also occurs gradually in the case of grasshoppers and is, probably, due entirely to the activities of natural enemies. Cases of a sudden cessation of an outbreak are relatively rare and practically always attributable to an epidemic of fungous diseases.

The difference between grasshoppers and locusts is apt, however, to become less striking during exceptionally great mass outbreaks of the former, when they exhibit certain peculiarities resembling the phases of locusts. Thus *Calliptamus italicus* must be classed as a non-swarming grasshopper, but when it appears in great masses, it is inclined to form larval bands that wander like those of locusts, and even something like a migration flight may be observed (Kiritchenko, 1926). It is not known, however, whether there is any difference in the morphology and coloration of the hoppers of these swarming forms and the usual one. Regular flights resembling emigration have also been observed in the Siberian grasshopper during exceptionally severe outbreaks. These facts indicate that a tendency to certain (at least, biological) changes in the direction of a swarming phase exists even in the solitary species, and this tendency is obviously stimulated by an increase in the density of population. Data corroborating this idea were obtained by Plotnikov (1927) in his breeding experiments when he observed that hoppers of various typically solitary grasshoppers, if bred in overcrowded cages, became darker in their general coloration. Particularly striking was the case of *Aiolopus tergestinus*, Charp., in which the hoppers are normally green, whereas crowding changed them into grey ones ; this case is very interesting, as this species never occurs in large numbers. The phenomenon reminds one still more of the phases, when we consider the results of the interesting experiments by Grassé (1923, see above, p. 70) with tropisms in solitary hoppers in which the energy of responses increased according to the density of population.

It would be a great mistake to regard as evidence of periodicity of non-swarming grasshoppers fluctuations in their numbers that are dependent on the current changes in the agricultural conditions of a certain area. For example, the last enormous outbreak of grasshoppers all over Siberia and in the Ural region was to a great extent due to the general decline in agriculture in that area during the revolution and civil war. We will return later to the connection between the outbreaks of grasshoppers and agricultural conditions ; in the meantime it is sufficient to state that this has nothing to do with the normal fluctuation in numbers.

Studies in the periodicity of grasshoppers must consist, in the first place, in a careful research into their ecology, particularly the influence of external conditions on their development. A very conspicuous place in the programme must be given to *quantitative* research on the inter-relations between grass-

hoppers and their natural enemies. This can be most profitably done by field studies on the ecology and numerical balance of grasshoppers and their enemies over a sufficiently long period of years. Particularly important would it be to conduct such investigations during the years when the grasshoppers are at a minimum, when it must be easier to appreciate the relative value of various factors in the maintenance of the normal equilibrium and in its disturbance. It is, perhaps, superfluous to say that investigations of this kind have never been attempted in any country.

CHAPTER VIII

THE TECHNIQUE OF CONTROL

The following chapter has, naturally, purely practical aims, namely, to give an idea of the methods of controlling locusts and grasshoppers with a view to selecting those that can be best recommended. The primarily practical character of this chapter has induced me to omit the historical part and to concentrate on the methods that not only are actually in use in different countries, but have also a promising future before them. I do not think it necessary, therefore, to enter into detailed discussion of those methods, which, although still widely used in some backward countries, must be regarded as dying out.

My desire to be practical induces me to avoid any very detailed treatment of the technique of some of the more recently introduced methods, though special attention is paid to their principles. This may seem to contradict the requirements of practice, but the technical details of methods still in a state of development are being constantly improved, while, on the other hand, the application of the same method can, and even must, vary according to the local conditions. It would be quite useless, for instance, to give full descriptions of the apparatus used for dusting by dry poisons ; this method has, apparently, a very great future before it, but for that very reason its technique is progressing very rapidly, and it would be obviously useless to describe in detail the machinery used last year, which is bound to be replaced by better models in a few months' time. Where a certain method is first introduced in a country on a large scale, detailed technical instructions must always be published that are in full agreement both with the apparatus actually in use and the local conditions. My task, as I understand it, is to make clear the fundamental principles of each method and to discuss its advantages and drawbacks, as well as to trace the lines of its possible future improvement. While the methods of control are now highly mechanised, I still maintain that the directions of further development must be determined by entomologists, who alone, with their knowledge of the insects in question, can discuss each method of control from all points of view, while the function of the technicians (constructors of apparatus, chemists, etc.) must be to satisfy the requirements of the entomologists.

In the selection of methods that are to be discussed more fully than others, I have relied on my personal extensive experience and on various (partly unpublished) information. In the comparison of various methods, many conditions must be taken into account. First of all, of course, the effectiveness

of a method must be proved, not only in the laboratory, but under actual field conditions as well. Then the question of the economic value of the method arises, *i.e.* whether the cost is justified by the results, and also how it compares with the cost of other methods. Some entomologists (and partly also the general public) are inclined to the opinion that locusts are enemies of agriculture to such an extent that they render all exact calculations of the cost of control quite unnecessary, and that all that can be done is to try and obtain the best possible results regardless of expense. This baseless idea is gradually giving way to a more reasonable one, namely, that the control of locusts must be based on economic calculations like any other agricultural work and that the expense must never exceed the possible damage. As regards expense, it is particularly important to emphasise the necessity of taking into account all actual costs, not only that of materials, apparatus, and administration, but also of the so-called " free " labour of the population, which often constitutes the heaviest item of expenditure.

Mechanical Methods

Under this name are somewhat artificially associated many different methods of control based on the mechanical extermination of insects by trampling, burning, etc. Practically all these methods belong to the past, and their application has been connected with forced labour of the population, which has naturally resulted in a strong reaction against them on the part of entomologists. Some mechanical methods are, however, still in use, and there are certain points in their favour, so that a wholesale condemnation of all such methods would be a mistake.

Destruction of Eggs.—In order to destroy the eggs in the pods, ploughing or harrowing the places where they are laid is often recommended. Theoretically the eggs are partly destroyed directly by the process or they become exposed to unfavourable climatic conditions and to natural enemies, chiefly birds. These purely theoretical reasonings are practically impossible to verify by direct experiment, and it is still more difficult to estimate the percentage which may be destroyed in this way or to calculate the relation of the cost to results. It is no wonder, therefore, that opinions differ greatly on the utility of this method.

It is obvious that it is not always possible to destroy the eggs. Thus it would be scarcely practicable, and certainly not worth while, to apply this method to large areas infested by eggs of swarming locusts in vast uncultivated areas. Though harrowing and ploughing are still used very extensively, for instance, in Spain for the control of the Moroccan locust, the reports, while proclaiming good results, also testify to the enormous cost (Lapazaran, 1925), though the cost of " free " labour is usually not included as it should be. While not denying that this method may be used occasionally, when, for instance, the area infested is very small and conveniently situated, I am quite convinced that no regular campaign can be based on destruction of the eggs.

Somewhat different is the position with regard to solitary grasshoppers. American entomologists especially insist on the usefulness of disking, as a

method of direct destruction of egg-pods, while it is presumed that the eggs from broken pods are unable to survive the winter. No exact experimental data exist on this point, and the recommendation appears to be based on theoretical assumptions, which is decidedly dangerous. From what has been stated in Chapter III, we know that eggs can withstand freezing quite well; the percentage of eggs actually destroyed by ploughing or harrowing cannot be very high, and the only remaining factor is the effect of birds and other casual enemies. All these are factors of very uncertain value, and the usefulness of the process still remains to be proved; only then can the question of its economic value be considered. In cases when ploughing or harrowing is of direct agricultural value (such as in alfalfa fields), there is every reason to apply it in the hope of destroying at the same time at least a certain percentage of the eggs.

A variation of the method consists in deep ploughing in order to bury the eggs under a thick layer of soil, but we know (p. 42) that the vermiform larva is able to emerge through great depth of soil, and this method is therefore useless.

To sum up, ploughing or harrowing cannot be recommended as a general and fundamental method of control either of locusts or grasshoppers. On the other hand, experiments are very necessary in order to find out the effect on the eggs of grasshoppers of various agricultural methods, which might be valuable from the agricultural point of view.

Associated with ploughing or digging with spades, is the collection of egg-pods as a method of control. This has been in great vogue in many countries, and in some it still remains one of the chief methods in use (Spain), mainly with regard to the Moroccan locust, the egg-pods of which, being very hard, are particularly adapted for the purpose. The pods collected are usually purchased at a fixed price, by weight or measure, or else the population of each village is obliged by law to produce a certain amount of pods. This method always involves an enormous amount of labour (usually not counted) and gives very indifferent results, since it is, of course, absolutely impossible to eradicate the egg-pods from a large area, and a large residuum always remains. Another very important drawback of this method is that it provides junior administrative officers with almost unlimited opportunities of exploiting the population, and it is to be hoped that it will be abandoned in the few countries where it has hitherto survived.

This exhausts the methods of destruction of eggs. Nothing more practical has ever been tried, and it would be difficult to suggest a method of dealing with eggs buried in the ground over a large area. There is, apparently, no hope for the development of control in this direction, and attention must be turned to the destruction of hoppers.

The *crushing of hoppers* is a method that has enjoyed a great popularity in the past and is partly still in use at present, though only in some backward countries where labour is cheap. Complicated machines have been constructed for the purpose, and of these the steel brushes on wheels used in Hungary (Jablonovsky, 1926) are perhaps the best. It is, however, quite impossible

by this method completely to exterminate bands of hoppers, as these are simply scattered as a result of it. This fact and the great cost of labour involved are the reasons for the complete abandonment of this method in practically all countries.

Collection of Hoppers.—We can safely leave out of consideration such primitive and unpractical methods as collecting the hoppers with entomological nets or larger appliances of the same kind drawn by horses. More interesting and useful are various types of American hopper-catching machines, and so-called hopper-dozers.

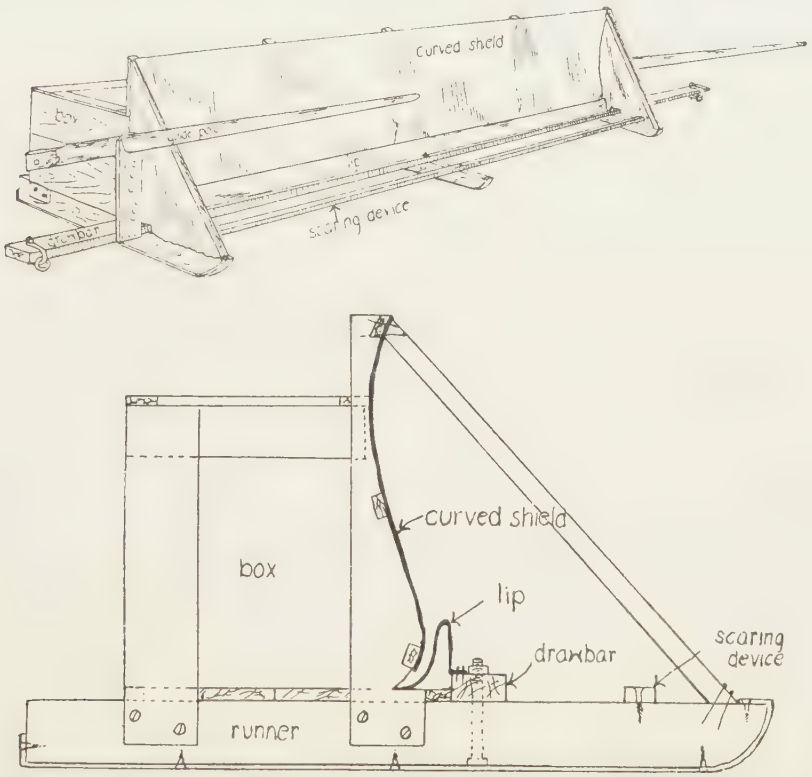

FIG. 74.—Grasshopper catching machine; perspective view and diagrammatic section (after Severin and Gilbertson).

The catching machine (Fig. 74) consists of a light wooden framework on which a shield of tin, or galvanised iron, is fixed vertically; when the machine is dragged along the field, the hoppers strike the shield and fall to the bottom of it, where they pass through a slit into a box at the back; to prevent them from jumping in front of the machine, a tin lip runs along the lower front edge, as may be seen in the figure. The machine may be of varying size and dragged either by men or by a pair of horses. The box is provided with doors, and the hoppers collected in it are then put into bags to be used as food for poultry. If not for immediate use, they must be dried.

Hopper-dozers are similar to the above, but are of simpler construction, since there is no need of a receptacle for the hoppers, which are killed by

means of oil. The dozer consists (Fig. 75) of a shallow pan of galvanised iron or tin containing crude oil and a vertical back sheet also of tin or cloth, the whole being fixed to a light framework and dragged along the field by men or horses.

It is clear that both these machines can be used only for the control of solitary grasshoppers, as it would be ridiculous to employ them against large bands of locust hoppers, though they are recommended for this purpose in some South American official instructions. Their use against solitary grasshoppers is also restricted to relatively small areas of privately owned land, where they may be very useful for periodic clearing of the field from scattered hoppers. On the other hand, for extensive organised campaigns in large outbreaks the expense involved in the construction of machines would be too

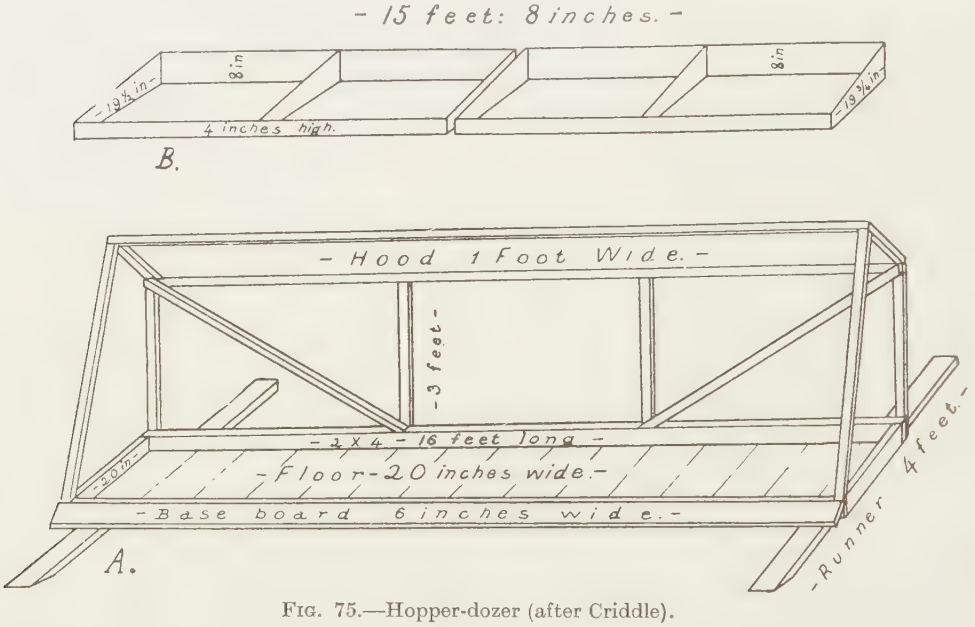
- 15 feet: 8 inches. -
8 in.
8 in.
- 19 ¼ in -
- 19 ¾ in -
4 inches high.
B.
- Hood 1 Foot Wide. -
- 3 feet -
- 2 x 4 - 16 feet long -
- Floor - 20 inches wide. -
- 20 in -
- Base board 6 inches wide. -
4 feet -
- Runner
A.

Fig. 75.—Hopper-dozer (after Criddle).

great, and the method cannot be compared favourably, either in efficiency or cost, with poisoned baits.

When it comes to comparing hopper-dozers and the catching machine, the advantage seems to be with the latter, since in addition to exterminating the hoppers, it also collects supplies of valuable poultry food.

Burning Hoppers.—Various modifications of this method are very popular for the control of locusts in dense larval bands. In the simplest form, the method consists of burning straw, etc., scattered over bands resting at night; the results are usually considered satisfactory, because the band after this treatment disappears as such; this is, however, an illusory result (I am speaking from experience), since only a small percentage of the hoppers is actually burnt, the rest simply scattering over a large area, only to congregate again after a day or so.

Further developments of this method have been in the direction of special

machinery. In Turkestan burning machines, consisting of a reservoir with petrol carried on the back, like a knapsack sprayer, have been in use for many years ; petrol from the reservoir is pumped into a long metal tube ending in coils surrounded by an iron muff. The muff is at first warmed in a fire ; the petrol is then pumped in, and it evaporates in the coil so that its vapour can be lighted at the outlet of the tube ; the resulting tongue of flame is then directed on to the hoppers. These instruments were used in great numbers, but were ultimately abandoned owing to the extreme danger to the men using them, there having been several fatal accidents.

Similar machines were used largely, but also abandoned, in North Africa, but quite recently this method of burning has been advocated by Vayssière (1921) who used army flame-throwers ; these produce tongues of flame up to 25 metres long and 3 metres wide. He found that, with the Moroccan locust in the South of France, this method gave excellent results, but only well-trained men must be employed. The cost, however, is very great, and is more than six times that of using poisoned baits ; this fact alone is sufficient to regard the use of flame-throwers and burning generally as methods without any future. It is very surprising, therefore, that flame-throwers are now being introduced into Palestine, Syria, and Iraq.

Ditches and Barriers.—One of the most popular methods of controlling locusts in nearly all countries before the advent of economic entomologists was the use of ditches. This method is based on catching larval bands in deep ditches with vertical walls. It can be either purely defensive, as when a ditch is made around a field to prevent bands of hoppers invading it, and in this form no objection can be raised against it ; it is clear, however, that a campaign of extermination of locusts over a whole area cannot be carried out in this way. For the destruction of locusts over large areas this method involved digging long trenches across the tracks of wandering bands, and a still further development led to *driving* the bands into prepared ditches. Since we know the blind determination of a moving band, which practically cannot be made to alter its direction, it is easy to realise what efforts were necessary to drive a band where it was required. The results are always very doubtful, though they may seem superficially satisfactory ; a large proportion of hoppers from the band manages to break through the line of beaters, others crawl under stones, clods of earth, etc., and only a portion arrives at the ditch and is buried there ; the band seems to have disappeared and is recorded as destroyed. Apart from the ineffectiveness of this method, it has a most serious disadvantage in that it requires an enormous amount of labour, both for digging trenches and for driving the hoppers. The whole long story of the struggle with locusts in Turkestan, for instance, right up to the time when the chemical method was introduced, is sufficient evidence of the complete failure of this method, and it has now been abandoned there for ever, though it is still in use in South America.

The use of *barriers* arose as a modification of this method. They were first evolved, apparently, in Cyprus, and were made of some fabric, cut in strips of sufficient width and placed vertically to form long screens. Extensive

trials in various countries, where these barriers were used, led to the abandonment of fabric in favour of iron sheets, as being more durable.

The barriers are made of narrow sheets of galvanised iron, 33 to 45 cm. wide (the width depending on that of the sheets as produced for other purposes and on the height to which the particular species of locust can jump), and varying in length. Single sheets are placed vertically and joined together to form a barier ; this may be done in several different ways, as is shown in the figure (Fig. 76).

The barriers may be used either for purely defensive purposes as when a cultivated plot is to be saved from moving bands of hoppers, but they are also extensively and very successfully used in several countries as the principal method of exterminating locusts on a large scale. The chief condition of success consists in an exact co-ordination between the disposition of barriers and the behaviour of locust bands. This idea has been particularly well elaborated during the recent German anti-locust campaigns in Anatolia (Bücher, 1918), where this method was applied on a very large scale and with great success. Without entering into all details, we will review briefly the main principles involved.

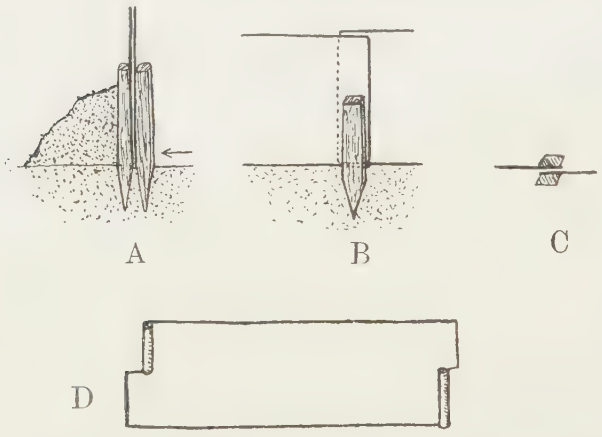

Fig. 76.—Different methods of joining iron sheets to form a barrier.—A, B, C, straight sheets fastened together by wooden pegs (section, side view and diagram) (after Bücher).—D, a sheet with the different halves of each end rolled to form a tube through which a round peg can be driven (after Borodin).

A band of hoppers in movement must be studied by a skilled observer on the evening before the operation, when it has not yet settled down for the night. This permits him to estimate the length of its front and also to find out the main direction of movement, which is usually resumed next day. When the direction of movement and its approximate velocity are established, the barrier may be erected. This should be done as near the band as possible, if it has already stopped for the night ; if the band is still moving, the barrier must be erected at such a distance that the hand would just have time to reach it before night. The erection of barriers may also be done in the morning, but the work must be completed before the morning movement begins, otherwise the hoppers will be disturbed and may change their direction. Barriers can be erected during movement in the day-time, but it is then very difficult to calculate the time necessary for the band to reach the barrier, which must be ready some time before this occurs.

When a barrier is ready and the band is moving towards it, there must be no men at the barrier, as this might frighten the band and alter the direction

of march. In many cases the barriers are combined with driving hoppers towards them, but this practice has proved to be most unsatisfactory in its results, besides requiring relatively enormous numbers of beaters. The key to the success of the method consists in the ability of the technical staff to understand clearly the situation and to erect barriers just where they are likely to be in the way of *freely moving* bands ; a barrier, favourably placed, cannot fail to catch absolutely the whole band to its last hopper.

Both the shape of barrier as a whole and its length depend on a number of purely local conditions and must be varied for each individual case. A general rule is that the barrier must form a straight line, at right angles to the direction of movement of the band ; the ends of the barrier in this case should be somewhat curved inwards to catch any hoppers that deviate from the direct line (Fig. 77). When a band is moving in a narrow column, for instance, along a ravine, the barrier may be made in the shape of a V open towards the swarm. Variations in the shape of the barrier may be almost

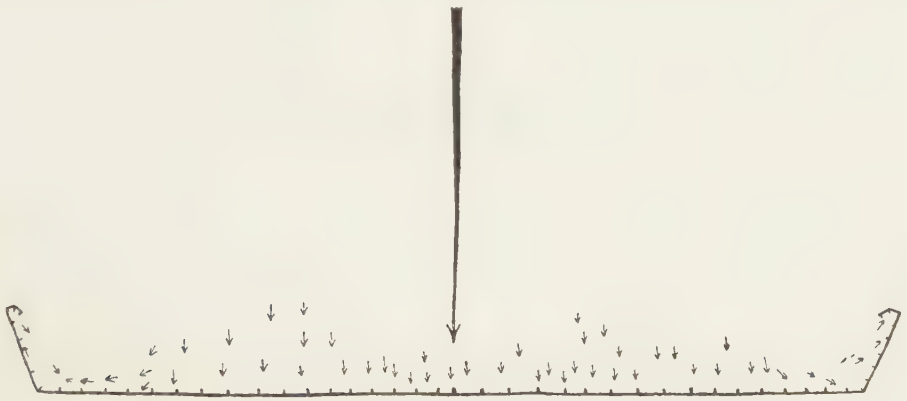

Fig. 77.—Diagram of a barrier with the ends curved (after Bücher).

endless, and an ingenious officer will always modify it to correspond with the particular situation.

To catch the hoppers arriving at the barrier and beginning to move along it, pits or ditches are dug close to the barrier, but at some distance from each other. The pits must have vertical walls, and it is sometimes useful to place strips of iron projecting over the edges, to prevent the hoppers that have fallen into the pit from crawling out (Fig. 78). If the digging of pits takes too much time, small enclosures may be made of the same sheets of iron as are used for the barriers ; earth is heaped along the outer sides of the enclosure, so that the hoppers can crawl over its top and tumble in (Fig. 79) ; in the centre of the enclosure a pole may be placed, and the hoppers will then climb it, so that finally a huge conical heap of hoppers is formed in the centre. Captured hoppers are simply buried and crushed ; when there are too many of them, it has been suggested (in South America) that they should be soaked in kerosene and burnt, but this does not seem to be absolutely necessary.

A barrier must be left standing until the whole band (or a series of them) is captured.

This method of using barriers has certain obvious advantages in a campaign against locusts in countries where there is a large proportion of uncultivated land ; if the conditions are reversed, it is usually out of the question

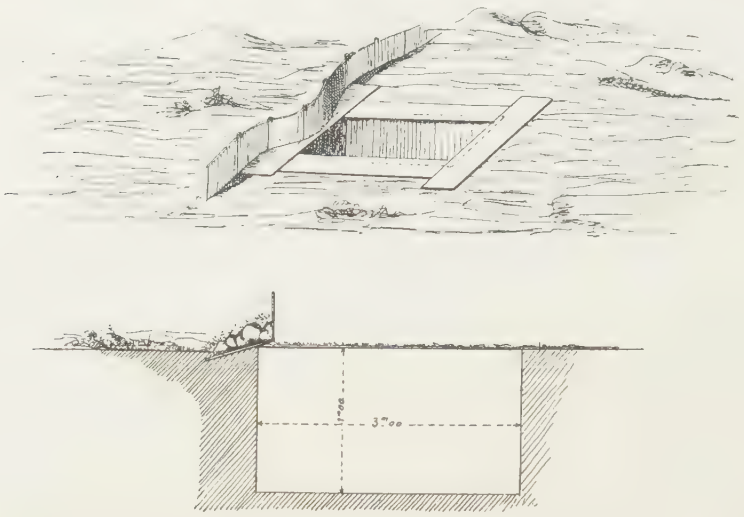

Fig. 78.—Above, a barrier in position with a pit ; below, section of a pit (after Bücher).

to erect barriers and to wait patiently for locusts to be caught by them. The amount of unskilled labour necessary for the transport of barriers and for their quick erection is very considerable ; consequently this method is a very expensive one if paid workmen are employed, and in these cases it cannot compete with the use of poisoned baits (or even spraying). Where the labour is requisitioned, the use of barriers may be cheaper and quite effective, but the demoralising effect of forced labour must not be forgotten. (We will return to this question in the next chapter.) In any case, the success of the method depends on having a suitable technical staff, the members of which must be not only well acquainted with the behaviour of locust bands, but also possess ingenuity in arranging barriers in the best way.

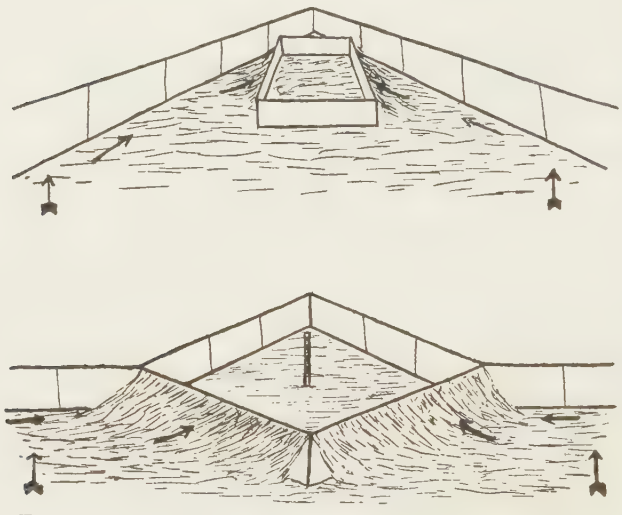

Fig. 79.—Iron sheet corrals (after the Official instructions, Mexico).

It goes without saying that barriers are not practicable against the solitary grasshoppers.

Chemical Methods

To this group are referred methods based on the use of various chemicals acting either as external or as internal poisons; they may be used either dissolved in water (or mixed with it in the case of insoluble substances), or in form of a powder, or as an admixture to baits, or, finally, as gases. The principles of the action of various insecticides are, of course, very different, so that the inclusion of them all into one group is merely for purposes of convenience.

External Insecticides.—External insecticides that will kill hoppers by contact are extremely popular in many countries. From the purely theoretical point of view, their use seems to be very advantageous, since it does not depend on the feeding of the hoppers, which has to be reckoned with in using internal poisons, and the method can be applied at any moment. In practice, however, the cost is a decisive factor, and this is distinctly against external insecticides as compared with internal ones. External insecticides comprise various mineral oils, kerosene, and allied substances, also soap and kerosene-soap emulsions, etc., and they are all more expensive than arsenicals, apart from the difficulties of their transport in large quantities. A further disadvantage of all contact insecticides is that they produce good results only in strong concentrations, such as are injurious to plants, and this prevents their use on cultivated land.

In certain cases, when a local ingredient for a suitable contact insecticide is obtainable at a low cost, and the work is done in an uncultivated country with sparse vegetation, contact poisons have a chance of competing successfully with internal ones, but only if the latter are applied in a liquid state, *i.e.* by spraying; otherwise the cost of application in poisoned baits will be always well below that of spraying with external poisons.

Actually contact poisons are now in use only in countries such as Spain, Portugal, and South America, where arsenicals are considered extremely dangerous both to man and domestic animals, though we shall see later how unfounded these fears are.

Internal Poisons.—The poisoning of insects by internal poisons may be done by two methods, either by spraying a poison on to their natural food or by offering them a specially poisoned bait.

In order to poison the natural food of Acrididæ, the vegetation is sprayed with a solution of arsenical compounds in water. This method is of historical interest, since it is due to its introduction that locust control in at least two of the greatest "locust" countries, Russia and South Africa, has been put on a really effective basis, and the possibility of complete and economical extermination of locusts on a large scale has been demonstrated repeatedly. At the same time it must now be admitted that spraying has no future before it. With all its great advantages, it has a number of serious drawbacks that prevent it from competing successfully with poisoned baits, these being both more effective and much more economical than spraying. The data obtained during a series of campaigns in various countries show

conclusively that the use of baits is applicable under any conditions and for any species, and this leaves no room for spraying. The latter is still used in some places, mainly owing to the conservatism of local organisations, which hesitate to adopt the bait method which is less known to them.

In view of all that has been said, I will only give a brief outline of the spraying method.

Amongst the arsenical compounds used for spraying, sodium arsenite and Paris green are most commonly used, the latter particularly in Russia (until quite recently, when it has been replaced by sodium arsenite), the former in South Africa. In the last-named country, the poison is prepared for use in a concentrated form in drums containing a strong solution which only requires the addition of water. This concentrated solution also contains molasses with a view to increasing the attractiveness of sprayed plants to locusts, but recent investigations by Mally (1923) have shown, somewhat unexpectedly, that this is quite unnecessary, since the locusts do not distinguish between plants sprayed with molasses and those free from it; consequently, the cheapest formula would be a simple aqueous solution of the arsenite.

It is unnecessary for our purpose to enter into a description of the apparatus used for spraying, since they are continually changing, nor is there any need to advise as to the kind of sprayer to be used, for the introduction of this method where it has not previously been in use is not advisable.

The actual work of spraying must be done in close agreement with the behaviour of the insects. If it is directed against non-migratory species that pass all day on the same spot, spraying can go on all day. On the other hand, when working with wandering bands of locusts, it must be always remembered that spraying is only effective if the actual plants eaten by the insects are sprayed. This condition renders useless all work in the day-time when the bands are on the move, and the most effective work is done in the evening, when the bands stop for the night and the plants they climb for rest and food can be sprayed. In practice, spraying work is done only very early in the morning or in the evening, and this makes the actual working day very short and increases the cost of the campaign enormously.

While I will not dwell on the obvious advantages of spraying as compared with mechanical methods, its disadvantages must be stated. The chief of these is its great technical complexity. It requires relatively very complicated machinery in large quantities, special field shops for repair, a skilled technical staff as supervisors, and trained workmen; all this makes it very complicated and expensive. Further, the results are intimately connected with weather, and frequent rain makes it almost impracticable and adds enormously to the cost. The last and perhaps the most important drawback is the necessity for sacrificing to the locusts a certain proportion of crops, since it is seldom possible to poison all bands on wild vegetation only; the damage done by the insects in these cases is usually slight, but the moral effect on the owners of the crops is very bad, as the plants have to be actually used as a bait for the locusts.

Further technical improvements in spraying are unlikely, and it is only to be expected that it is everywhere giving way to the use of poisoned baits, which are free from nearly all these disadvantages and possess some special merits of their own.

Poisoned Baits.—The use of poisoned baits is based on the positive chemotropism of ACRIDIDÆ towards certain substances that are more attractive to them than their normal food plants.

Since this method is still in the process of a vigorous evolution and improvement, and since it clearly has a great future before it, we must discuss the details of its technique and application in full. The main purpose of this discussion is to point out such details as require further experimental study and elucidation in order to make the method still more effective and lessen its cost.

A bait consists of three component parts: carrier, poison, and attractant. The bait is prepared by mixing these ingredients in certain proportions and scattering it on areas infested by ACRIDIDÆ, in order to divert them from crops. We will now discuss each of the component parts separately with a view to comprehending our present knowledge concerning them and the nature of the problems connected with them.

At first it was only natural to use green vegetation as a carrier for baits, and cut grass, lucerne, etc., moistened with a liquid insecticide has been used on many occasions and always with good results, especially against locusts. The difficulty of procuring suitable plants in large quantities and the amount of labour needed for cutting and transportation present, however, serious objections, and this form of bait can only be used where the conditions are particularly favourable, while it cannot be recommended for general use.

The next step in the evolution of baits led to the use of *animal manure*. Direct observations in the field showed that many ACRIDIDÆ congregate in large numbers on fresh horse droppings, and the Canadian entomologist, N. Criddle, evolved a bait, called the Criddle mixture, composed of horse manure, salt, and arsenicals. This type of bait has been used on a large scale in Canada and Siberia with very good results. Horse manure is particularly suitable for the purpose; cow dung may be used as an addition, but is better omitted. It is not necessary to use fresh droppings, dry manure, without an admixture of earth or straw, being the best. Siberian entomologists recommend breaking the dry manure into small particles; the latter must be, however, not too small, but somewhat like coarsely cut tobacco. No detailed experimental work on manure bait is known to me, but Berezhkov (1923) states that the results obtained with it in field work on a large scale do not differ from those with bran baits.

Best known as a carrier in baits is *bran*. Practically all authors insist on the necessity of using wheat bran, though no exact experimental evidence is known to me on this point.

American and Siberian entomologists arrived independently at the idea of using *sawdust* as a substitute for bran in baits. According to Ford and

Larrimer (1921), a mixture of bran and sawdust (half and half) attracts 36·9 per cent. more grasshoppers than sawdust alone ; a bait of bran alone is, it is true, 14 per cent. more attractive than the mixture, but the cost is, of course, much higher. When compared with horse manure, sawdust proved to be more attractive, even without the addition of bran. Berezhkov (1922) believes that these differences are of but little practical value in the field, as in his experiments the mortality of grasshoppers on the fifth day after scattering the baits was : on the plots with bran, 97–99 per cent. ; with sawdust, 92–99 per cent. ; and with manure, 90–98 per cent. The same author (1923) points out that sawdust has a special advantage in that the bait prepared with it is very resistant to weather and retains its effectiveness for ten days after application, while bran is effective for 7–8 days and manure for 5–6. Since these data are all based on baits prepared with soluble sodium arsenite, the difference must depend on more complete absorption of the solution by sawdust. Taking all these facts into consideration and having regard to the considerable lowering of cost by substituting sawdust for at least part of the bran, it seems unreasonable to insist on the use of pure bran baits, at any rate in countries where sawdust is easily obtainable.

It would be, however, premature to recommend sawdust as carrier for baits for all species of Acrididæ in all countries, since, for instance, Moritz-Romanova (1925) found that hoppers of *Locusta migratoria* do not take baits of sawdust. Equally unsatisfactory results were obtained with sawdust baits against *Calliptamus* in Turkestan by Arkhangelsky (1923). In both cases sawdust was used pure, not as an addition to bran.

Ford and Larrimer (1921) have studied the question of the kind of sawdust and found that pine sawdust (both pure and when mixed with bran) is less attractive than sawdust from red gum or hickory, and the reason for this deserves further study.

Chaff, which is cheaper than bran, can be also used in baits, at least as an admixture to bran ; it has been used in field work in Altai, but good results were obtained only with wheat and oat chaff, that of millet giving negative results (Berezhkov, 1923), as also did rice chaff in experiments with *Locusta* (Moritz-Romanova, 1925).

In the cotton-producing countries it may be possible to use cotton-seed meal, which has been found effective against *Calliptamus* (Arkhangelsky, 1923) and *Locusta* (Moritz-Romanova, *l.c.*) ; the last-named points out, however, that the great weight of the meal makes it a very expensive item of transport, while the quantity, by weight, must be also greater than in the case of bran.

Of other carriers may be mentioned *beetroot*, which was found very effective by Paoli (1919). It was used in small pieces, which absorb three times their weight of the poison solution and retain their effectiveness for a long time. Fairly good results were obtained also in America with the pulp from beet-sugar factories, which proved to be 66 per cent. as attractive to grasshoppers as bran, but it dried up much faster and did not scatter well (Swenk and Wehr, 1923).

I will not discuss the results obtained in various experiments with other less common substances. There is no doubt, however, that in some countries (particularly in the tropics) other local materials can be found, which will prove to be satisfactory. An entomologist beginning to work with baits in a new country must not follow blindly the formulæ obtained in other countries, but ought to try and find the cheapest and most suitable local materials. The first and the most important practical requirement of a good carrier is, of course, low cost and its availability in large quantities on the spot. Next follows its attractiveness to the insects, but this we will discuss later, when dealing with the problem of the attractiveness of baits in general.

The factor deciding the suitability of material as a carrier for baits is its physical properties, particularly its ability to absorb water. This is of the first importance, because the attractiveness of the bait depends to a great extent on how long it retains its moisture. This quality has also special importance when soluble poisons are used in baits. It is clear that to obtain a bait with a constant percentage of poison, the strength of the poison solution must be correlated with the quantity of water absorbed by a unit of weight of a given carrier. This question has been specially studied by Paoli (1919), who prepared the following table :

Material.	Absorbs water in per cent. of its own weight.	Percentage of solution to obtain bait with 4 per cent. of poison.
Broken wheat grains	30	13
Bran	70–90	5
Ground maize cobs	125	3·2
Chopped beetroot	300	1·3
Sawdust	70–100	4–5
Broken plum kernels	35	11·4

In experiments with all these materials, it was found that beetroot, which is the most hygroscopic, gave the best results and preserved its effectiveness longest. In practice Paoli used a bait composed of 7 parts broken wheat, $1\frac{1}{2}$ parts bran, and 1 part ground cobs, and this combined satisfactory physical properties with cheapness.

The question of the quantity of absorbed water has also been studied by Moritz-Romanova (1925), who, however, simply tried to find out the quantity of water necessary to prepare a sufficiently moist and easily scattered bait. The results, when expressed in percentages, are :

Material.	Absorbed water in per cent. of its own weight.
Manure	145–150
Sawdust	100–125
Wheat bran	90–95
Rice chaff	90
Rice bran	55
Meal of cotton-seed cake	40–50

The figures by Moritz-Romanova are all relatively higher than those given by Paoli, but this simply depends on the fact that Paoli gives figures for the absorbed water only, while the preparation of bait requires more water than this.

Moritz-Romanova also paid some attention to other physical properties of carriers, particularly to the ease with which a bait can be scattered, without forming large lumps or breaking up into too small particles. In this respect cotton meal has proved to be better than bran. Wheat bran scatters better with the addition of about 10 per cent. of millet or rice chaff or sawdust, while pure bran is sometimes too sticky ; the latter is a special property of rice bran, which cannot in consequence be used alone.

In summing up our review of carriers it must be admitted that very little has been done so far towards exact investigation of the physical properties of these materials as regards their suitability for baits. The bulk of the experiments have aimed at a purely empirical valuation of the advantages of one material over another without any attempt to find out the reasons for them. At the same time, as stated above, in practice it is quite easy to find a suitable carrier in any country, and the local conditions are the chief factor in making the choice.

As regards the *poisons* used in the baits, practically all previous research refers to arsenical compounds, and there are few data on other poisons. All the experimental work has been done by American entomologists, the comparison between arsenical compounds being made on the basis of efficiency (percentage of kill), attractiveness, and cost. Ford and Larrimer (1921*a*) at the West Lafayette laboratory studied relative value in baits of Paris green, white arsenic, and crude arsenic. The best results were obtained with the white arsenic, which produced a mortality of 90·9 per cent. when the strength used was $\frac{3}{4}$ lb. to 25 lb. of bran ; an increase in strength was followed by a decrease in mortality, probably because of the lower attractiveness. Paris green gave the best results, 85·5 per cent. mortality when the strength was 1 lb. to 25 lb. bran (and 79 per cent. at $\frac{1}{2}$ lb. strength), while higher doses were again less efficient. Crude arsenic produced 77·4 per cent. mortality, with $1\frac{1}{4}$ lb. to 25 lb. bran. Direct comparison of all three poisons, applied at their optimum strength and under optimum conditions, showed that the differences between them are very slight and of hardly any practical importance.

Experiments in Nebraska (Swenk and Wehr, 1923 ; Swenk, 1927) were conducted with the same three poisons and with calcium arsenate. The results can be summarised as follows. Baits containing white arsenic are 8–10 per cent. more attractive than baits with Paris green and are very much more attractive than baits with crude arsenic ; calcium arsenate is 18 per cent. more attractive than Paris green. As regards their killing efficiency, crude arsenic acts more quickly than any other poison tested ; it is also the cheapest, but its use cannot be recommended owing to its slight attractiveness. Paris green is too expensive for use on a large scale, costing over three times as much as white arsenic, while only 5–6 per cent. more efficient. Calcium arsenate, which about equals white arsenic in efficiency and surpasses

it in attractiveness, has the disadvantage that it is about one-third more expensive. On the whole, the authors recommend for field use a fine light grade of white arsenic if the baits are to be prepared by the dry method (see below). For baits prepared with a liquid poison, arsenite of soda, made by boiling white arsenic and sal soda, is a poison highly recommended, as it proved to be more efficient and cheaper in use than any of the dry poisons. Corkins (1923) also prefers sodium arsenite (commercial grade, obtainable as a weed killer) to any other poison ; the optimum strength was found to be one pint of sodium arsenite (containing 1·01 lb. of As_2O_3) to 100 lb. bran. This very small quantity of poison is probably explainable owing to its very even distribution, because it is mixed wet, and also because it is more readily digested by the insect owing to its complete solubility.

This practically exhausts the exact experimental data on various arsenicals in baits. Further work must, apparently, be directed mainly to the elucidation of direct causes of differences in the action of various poisons ; mere tests, without more elaborate studies in the action of poisons, cannot contribute materially to any progress with baits.

One point about arsenicals has been omitted by American entomologists, and this is the question of how long baits containing various poisons remain effective in the field. Sevastianov (1915) in his experiments with baits for the Moroccan locust in Turkestan, used " locusticid," Paris green, and London purple, and his conclusion was that insoluble poisons have a definite advantage over soluble ones, since the poison in the baits prepared with them remains even after rain. He particularly recommended London purple, which proved to be a sufficiently effective poison, while being one of the cheapest arsenical preparations on the market. Unfortunately, Sevastianov's work has remained unnoticed by later students of the problem, and it is to be hoped that the question of the relative value of soluble and insoluble poisons will be subjected to special investigations.

For practical purposes it is now possible to recommend the use of sodium arsenite $\frac{1}{4}$ to $\frac{1}{3}$ lb., white arsenic $\frac{3}{4}$ lb., or Paris green $\frac{1}{2}$ lb., to 25 lb. bran. It is perhaps worth mentioning that the strength to be recommended has an importance, apart from the cost, since experiments show that an increase of the amount of poison above the optimum strength results in a decrease in the attractiveness of baits. The dosage of poisons usually applied in the field work in the United States and Canada is higher than is necessary.

As has already been stated, hardly any work has been done on poisons other than arsenicals. Moritz-Romanova (1925) tested barium chloride, but the results with *Locusta migratoria* were negative. Recently considerable interest was aroused in the possible use of fluorine compounds in baits. Ripley (1924) first called attention to the toxicity of sodium fluoride which he tested against the Brown Locust in South Africa, both in baits and for spraying. Experiments in the laboratory showed that sodium fluoride is only slightly less effective than sodium arsenite, while being very much cheaper (it is obtained as a side product during the commercial process of extracting aluminium from criolite). At the same time, laboratory experiments by E. Hargreaves (Bull.

Ent. Research, XV, 1924, p. 56) proved that calcium fluoride, *i.e.* fluorspar, which is also a very cheap product, has a considerable toxicity for various insects.

Somewhat more detailed experiments with these poisons were made by Langford (1926), especially in baits for grasshoppers. His laboratory experiments with *Melanoplus femur-rubrum* gave the following percentages of mortality from different poisons :

Sodium fluosilicate	1 lb. to 52 lb. of bran	100 per cent. (after 4 days)
Sodium fluoride		92 ,, ,,
Paris green		98·7
White arsenic		98·2
Sodium arsenite		96·5
Control		30·3

Very good results were also obtained by Langford in field tests of fluorine compounds in baits.

These data can be, of course, regarded only as preliminary, but they suggest the possibilities of finding new and cheaper poisons, deserving of serious investigation.

Let us turn now to the problem of the *attractants* which are added to baits.

It was assumed from the very beginning that baits are eaten by locusts and grasshoppers, only because something specially attractive is added to them. Spraying in South Africa at first was based on a sweet insecticide, and only after many years of use was it discovered (Mally, 1923) that there is no need to sweeten the poison. The same assumption that Acridids would not eat a bait if it is not sweet, has induced practically all entomologists to recommend the addition of molasses to it. Recently, however, some experimental work in America, as well as extensive field practice in Siberia (where the use of molasses is out of the question for economic reasons), has proved that the addition of sweet substances to baits cannot be considered absolutely necessary, and very good results can be obtained without them. Moreover, some authors have obtained experimental data that tend to show that molasses not only does not increase the attractiveness of bait but in some cases that a bait is even more attractive without it (Swenk and Wehr, 1923 ; Morill, 1919). Other authors insist on the usefulness of molasses ; thus, Ford and Larrimer (1921*a*) found that baits with molasses were 8 per cent. more attractive than without, though there was no difference whether one or two pints of the molasses were used to each 25 lb. of bran. Parker (1924) also obtained results in favour of molasses, which increased the attractiveness of baits prepared with aromatic substances ; unfortunately, his series of experiments did not include baits without any attractants for comparison.

On the whole, the value or otherwise of molasses remains uncertain. Even if it actually increases the attractiveness of bait, the question remains whether the increase justifies the much higher cost. In calculating this, it is particularly important to take into consideration, not the market cost of molasses, but that in the area where the anti-locust work is being carried on. In the great majority of cases, these places are so far from the centres of a sugar

industry that the expense of transport greatly exceeds the initial cost of the material.

In addition to molasses, or independently of it, various aromatic substances have been used as attractants in baits. In America, particularly, lemons and oranges are very widely used and recommended for the purpose, though experimental data on the value of aromatic substances are very contradictory. Thus Ford and Larrimer (1921) proved that various fruit attractants were not only useless, but that baits with some of them were even less attractive than with bran alone. On the whole, molasses was found to occupy the first place, molasses and apples the second, and wet bran (control) the third.

Detailed experiments by Parker (1924) resulted in the following sequence of attractiveness of various aromatic substances, which in all cases were used in addition to molasses : amyl-acetate, butyl-acetate, propyl-acetate, lemons, apple extract ; in all cases better results were obtained with molasses than without it, except in the case of lemons, which gave better results without molasses.

Experiments in Nebraska (Swenk and Wehr, 1923), where molasses was found of little value, gave results favourable to lemons and oranges, but their high cost makes them unsuitable ; amyl-acetate gave good results here also, but the increase in attractiveness appears to be hardly justified by the higher cost.

The action of aromatic substances varies according to the stage of the grasshoppers, younger hoppers being more susceptible to odours than older ones and especially than the adults (Ricker, 1919).

A special category of attractants is presented by the bodies of the Acridids themselves. The South African official instructions (South Africa, 1921) recommend the use of baits in which freshly collected and partly crushed hoppers are used as a basis ; observations show that the crushed insects are greedily devoured by their comrades. It would be very interesting to test on a large scale baits of bran or sawdust, with crushed hoppers as an addition. Equally important would it be to try and discover the chemical nature of the substance which acts in this case as an attractant. This example shows that attractants are not confined to vegetable oils or extracts, and still more incorrect is it to restrict the choice of them to substances that have an odour that is pleasant to man.

In concluding our survey of attractants used in baits, it must be pointed out that all experiments on them are to a great extent superficial as regards the way in which it is hoped by entomologists to solve the problem. Indeed, we have to deal in this case with the chemotropism of certain species of Acrididæ, and it is obvious that all experiments must be put on an exact chemical basis, instead of comprising haphazard tests of the widest possible assortment of substances. It would be necessary, first of all, to find out which groups of aromatic substances are attractive at all, and it should then be possible gradually to narrow down the choice by studying systematically one group after another. There is no doubt that this method should lead to results of great practical

importance. Of course, it is not impossible to discover a suitable attractant by pure accident, but this empiric method is not very hopeful, since the range of substances, which may act as attractants, is very wide. This was demonstrated by the work of entomologists in South India, who found that a bait containing mango fruits was very attractive to grasshoppers ; an analysis of the fruit showed that the odour of mango is due mainly to terpene, and that one of the terpenes (terpinol) proved to be an excellent attractant (Ballard and Muliyil, 1921).

Apart from aromatic substances, the attractiveness of baits is influenced by other factors. In the first place, as I have already pointed out, baits of bran and water only are often very effective, and it remains yet to be discovered to what their attraction is due—to the water or to the bran. The latter has a strong odour of its own, the nature of which has not been studied, while it might serve as a basis for finding out the actual chemical substance involved. That water can act as an attractant there is no doubt, the need of Acridids for water being usually very great (see Chapter IV), so that in hot and dry climates baits attract mainly because they are damp. Drying up of the baits usually lowers their attractiveness, but does not suppress it altogether, since not only bran, but even manure and sawdust baits are eaten by grasshoppers when dry (Berezhkov, 1922).

The fact that damp baits, as compared with dry ones, have greater powers of attraction, raises the question of preserving them from drying out when scattered. Most American entomologists recommend the addition of common salt (about $\frac{1}{4}$ lb. to 25 lb. of bran). The experimental data on this point are, however, somewhat contradictory. Thus, Ford and Larrimer (1921) obtained results showing that salt decreases the attractiveness of bait by about 23 per cent., while Parker (1924) proved that salt not only increases the attractiveness of baits containing aromatic substances, but gives even better results than some of the latter. Swenk and Wehr in Nebraska (1923) found that salt decreased the attractiveness of baits for the younger hoppers, but slightly increased it for the adults. Siberian entomologists have arrived at the conclusion that the addition of small quantities of salt does not help in maintaining the bait in a damp condition, while larger quantities make it unattractive (Berezhkov, 1923). Obviously more information on this point is required.

Swenk (1927) tried adding calcium chloride to baits to prevent them from drying out too rapidly, and found it useful in hot and dry weather, but the high cost of this substance makes its wide use impracticable.

To sum up our somewhat lengthy review of the composition of baits, the substances recommended for carriers are bran, sawdust, horse manure, and other suitable local materials ; in many cases a combination, for instance, of bran with sawdust may be very effective. As poisons, sodium arsenite, white arsenic, and Paris green may be used. The addition of molasses or aromatic substances (particularly amyl-acetate) is not necessary, but may prove useful ; the addition of salt cannot be definitely recommended.

On the whole, it is obvious that our knowledge of baits is only in its infancy,

and a great amount of experimental work must be done. In connection with this work, in which entomologists in all countries will have to take part, it may not be out of place to describe briefly the *methods of experiments with baits* as they have been carried out by previous workers.

A good example of experimental work with baits is given in the Nebraska reports (Swenk and Wehr, 1923). For the experiments a level place was selected in a field well infested with grasshoppers. Small batches of the baits were made up in accurate proportions by carefully weighing all ingredients, and two pounds of each bait to be tested were placed in a round tin pan, ten inches in diameter and one inch deep. These pans were arranged in a wide circle, and the vegetation around each pan was cleared in order that the pans could be seen from a distance. The observer then retired to a sufficient distance (20 to 30 feet) so that the grasshoppers would not be affected by his movements, and made, with the aid of a binocular field-glass, counts of the numbers of grasshoppers on each pan every five minutes, continuing this throughout the day. The relative position of the pans was changed every two hours in order to equalise the chances. The total number of grasshoppers observed on each pan during the whole day was taken as indicating the relative attractiveness of the baits tested. Since it was difficult to observe and count only the grasshoppers actually feeding on baits, it was found more practicable to count all grasshoppers seen on the pan or within six inches of it.

An objection to this arrangement lies in the fact that grasshoppers may be partly attracted to pans not by baits but because of their thermotropism, which usually makes them select open and somewhat raised spots. To test this, when experiments were made with pans simply filled by earth, the number of grasshoppers on them proved to be about one-third of those attracted by the best bait, and very nearly that attracted by the least effective bait. The authors concluded that these visits to pans due to causes other than the attractiveness of baits may be ignored, but it would be more correct to include in the series of experimental pans some without baits and to introduce a corresponding correction in the results.

Attempts to replace tin pans by wooden boards disclosed that in this case a very serious mistake may arise, because the boards in the sun's rays become much warmer than the ground (or tin pans), and the grasshoppers collect on them owing to their thermotropic effect (Parker, 1924).

Where experiments aim at finding the effectiveness of various poisons in baits, the following method is applied. A definite quantity (by weight) of each kind of bait is taken, and separate plots sufficiently isolated from each other are treated ; the plots selected must, of course, be both equal in size and similar in their conditions. Twenty-four hours after scattering the baits, one or two hundred grasshoppers from each plot are collected by " sweeping " and placed in separate cages with fresh, not poisoned, food. After five days a count of living and dead grasshoppers in each cage is made, and this gives the percentage of mortality ; it is necessary, however, to correct the latter by keeping a special control cage containing grasshoppers from an unpoisoned field, since a certain mortality always occurs in cages.

A supplementary method of estimating the efficiency of baits consists in the periodic "sweeping" of grasshoppers in treated fields, the number of grasshoppers caught in a given number of sweeps being counted; in this way, an idea may also be obtained of the length of time during which the bait is effective in the field (Berezhkov, 1922).

Let us now discuss the *technique of preparing baits* during the actual field work. This may be done by either the dry or the wet method.

The dry method is the best for insoluble poisons, since it ensures a better distribution in the bait. Mixing the bait by the dry method is either done simply on a good floor, or in a large box, washtub, etc., but when large quantities of bait are wanted, special mixing machines are of the greatest use. The simplest type of such machines is recommended by the Oregon Agricultural College (Fulton, 1920), this being simply a wooden box that turns on a shaft;

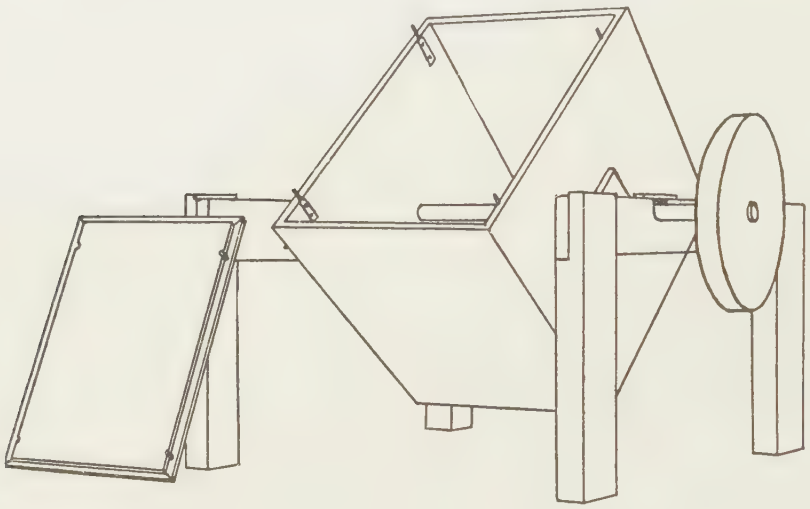

Fig. 80.—Oregon poison bait mixer (after Fulton).

the dimensions recommended are 4 ft. × 4 ft. × $2\frac{1}{2}$ or 3 ft. (Fig. 80). The mixer can be turned by hand, or by horse power, or even by a small motor. The speed should be about 35 revolutions in a minute, as the bait does not mix well if the box revolves faster than this.

After the bran is mixed with the dry poison, the mixture is turned out and the water (and attractants, if any) gradually added, while the bait is being thoroughly mixed. It is difficult to give the proportion of water, as it depends on the quality of the bran or other carrier used. In any case, the bait must be sufficiently damp, but must not form lumps, and a handful of bait, after being pressed in the hand, must on opening the hand crumble easily, so that it will break up into small pieces.

When soluble poisons are used, the wet method of mixing baits may be preferred, though it has no special advantages. It is done simply by mixing thoroughly all the ingredients with an aqueous solution of the poison.

The technique of the *distribution of baits* is very simple. In most cases

the bait is scattered by hand, each operator carrying his supply of bait in a pail, or in a sack strapped over the shoulder ; each operator walks along the field and scatters the bait by broadcasting it in the same way as is done when sowing by hand (Plate VIII, Fig. 2). In some places, particularly in Canada, the use of a special seeder (devised by Parks, 1917) is recommended. This (Fig. 81) consists of a canvas bag strapped over the shoulders of the operator and fitted with a feeding device consisting of a canvas sleeve and swinging tube made of tin or galvanised iron. The tube is 28 inches long, $2\frac{1}{2}$ inches in diameter at the upper end and $1\frac{5}{8}$ inches at the lower. Over the opening at the lower end are soldered two short wires, bent in the shape of a U, crossing each other at right angles about an inch below the opening of the tube. These wires are soldered together where they cross, and their purpose is to break the bait into small pieces as it leaves the tube, while it is swung backwards and forwards in front of the operator.

The quantity of bait to a unit of area must vary under different circumstances, but in the case of solitary grasshoppers it is fairly constant, since experiments have shown (Ford and Larrimer, 1921*a*) that very little difference exists in the percentage of kill obtained from applying baits at different rates per acre ; the best results were obtained with $7\frac{1}{2}$ lb. per acre, while a larger amount is practically useless and does not justify the increased cost. A general recommendation is to use from 5 to 10 lb. of bait to an acre. In practice, however, much more bait is used, because it is usually not distributed sufficiently thinly and evenly, as it should be, in order to cover the ground more thoroughly and, at the same time, to avoid any risk of poisoning domestic animals, which may pick up large lumps, whereas they cannot find properly scattered bait.

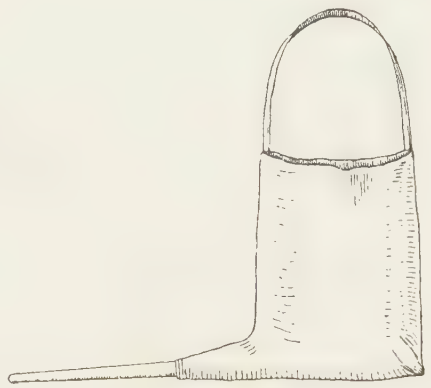

FIG. 81.—Poison bait seeder (after Gibson and Criddle).

Baits may also be scattered from a waggon or motor-car ; sometimes broadcast grain seeders are used for the purpose. Whatever method is used, it must be remembered that the object is to distribute the bait thinly and evenly over the whole field.

When working with locusts, the methods of distributing baits must be altered, since it is only rarely that large areas have to be treated, and the whole work is concentrated on poisoning distinct bands. In this case each band must be treated separately by scattering bait over it in the evening, when the band has stopped for the night, or very early in the morning. It is quite possible, however, to apply baits even in the day-time, when the bands are on the move, since at least in the case of the Moroccan locust, it has been proved that the bands can be stopped by a strip of bait placed in front of

them (unpublished data by M. M. Siazov, from his experiments in Transcaucasia).

The success of distributing baits depends to a great extent on the *time of the day* when it is done. This applies not only to locusts, but also to solitary grasshoppers. Usually it is recommended that the baits for the latter should be scattered in the evening and early morning, but Parker (1924) pointed out that it is more correct to regulate the time of scattering the baits by temperature, not by the clock, the time of feeding depending entirely on this factor. His experiments established that baits for *Camnula pellucida* should not be distributed when the temperature is under 20° C., or over 26·6° C., while the best results are obtained at temperatures ranging from 22·7° to 25° C. Since the temperature limits of activity are very similar in various species of ACRIDIDÆ (see p. 80), these figures may be applicable to other species, but it would be better to find out the most effective temperature for each species by direct observations.

Another very important point that may seriously affect the results of work with baits is the age of the insects. American data supply the evidence that the chemotropism of hoppers in early stages differs considerably from that of older hoppers. As a result, the younger hoppers are more easily attracted by baits containing aromatic substances, which have a less marked effect on the older ones. Indeed, it is quite possible that the attractants for young and older hoppers may be different, but no definite information exists on this point.

It may be remarked, incidentally, that the effect of poisons in the baits is different on hoppers and adults, the latter showing symptoms of poisoning and dying more quickly than the hoppers (Swenk and Wehr, 1923). In any case, however, the insects eat very little after taking poisoned bait (Ford, 1921).

Concluding our discussion of the bait method, it may be useful to summarise its advantages. The first of them is its cheapness, due to the very small amount of work necessary per unit of area and to the practical absence of expenditure on apparatus. On the whole, the cost of baits may be estimated as about one-third to one-fourth that of spraying, which was formerly considered the cheapest of all methods. This applies, of course, to cases when all work is paid for, but work with baits can be done to a very large extent by voluntary work on the part of farmers ; this is impossible with spraying, which requires trained operators. Another advantage of baits is their effectiveness under any conditions of vegetation and ground, whereas spraying or the use of barriers are often impossible owing to these conditions being unsuitable. Meteorological factors also affect very little the work with baits, while spraying is very often impossible owing to rain, and no work can be done with barriers when locusts are not on the move owing to bad weather.

The greatest advantage of the bait method is its simplicity, which makes it very easily understood and appreciated by the public, which is not the case with other methods.

Objections to the bait method usually consist in the risk of poisoning domestic animals, but extensive experience in North America and various

parts of Russia has proved that no cases of poisoning stock can occur if the bait is scattered in small fragments, as it should be ; indeed, all known cases of poisoning domestic animals have been invariably traced to carelessness on the part of operators in leaving prepared bait where it was accessible to them. Neither is there any danger to the operators themselves, provided that they wash often, especially before meals.

All these features of poisoned baits make their use unquestionably the best and most effective method of all, and there is no doubt that they will be in wide use for many years to come, and will replace all other methods. They are particularly important in the control of solitary grasshoppers, more especially as other more recent methods, which will be discussed next, are best suited to locusts. In all new areas, where the control work is to be organised on a firm basis, a complete success can be guaranteed with the bait method, and it can be adapted to any kind of local conditions.

Dusting by Dry Poisons.—The application of dry pulverised poisons for the control of various pests has a fairly long history, particularly in the United States, but it is only quite recently that dry poisons have been tried in the control of ACRIDIDÆ. The first attempt was made in South Africa (Mally, 1923), where some experiments were made with powdered sodium arsenite with a view to avoiding the use of water, which is one of the main items of expenditure in spraying in desert countries. These proved that the dry poison is effective as an internal insecticide, and it was discovered at the same time that it can act also externally, locusts dying without eating dusted plants, if some poison got on their body. Indeed, it was sufficient to dust the antennæ with poison to kill a locust in four or five hours. The dusting was done by hand bellows, and no data were published illustrating the relative cost of dusting and spraying.

More detailed studies of dusting were made in the Northern Caucasus in connection with the use of aeroplanes against locusts (Sviridenko, 1926 ; Korotkikh, 1927 ; Parfentiev, 1927 ; Vyshelessky, 1927). These experiments proved that dry sodium arsenate undoubtedly acts as an external poison, since it was sufficient (in laboratory experiments, Sviridenko) to put some arsenate with a brush on the body of hoppers to kill them within twenty-four hours ; an analysis of the stomach contents proved that there was no trace of arsenic there. On the other hand, Vyshelessky records observations, from which it appears that hoppers of the Migratory Locust avoid vegetation dusted with sodium arsenate and Paris green ; plants dusted with calcium arsenate were eaten almost as readily as those that were not dusted at all, but this has proved to be a very feeble poison for locusts.

In any case, the general opinion of all the above authors is that dusting has proved to be eminently satisfactory. It remains, however, to be proved that dusting is not only as effective, but also at least as cheap as other methods. Theoretically, dusting has an enormous drawback owing to the necessity of using special apparatus, whereas practically none is required for baits. On the other hand, however, it is possible to reach, by dusting, places that are quite inaccessible with baits, as for instance the reed beds that are frequented by

bands of the Migratory Locust. This becomes possible by using aeroplanes as distributors of poison dust.

From experiments in the Caucasus with aeroplane dusting against locusts, the commission, which conducted them, concluded that this method has great possibilities, particularly against the Migratory Locust in its permanent breeding areas, though, as already stated, the data as to the cost are inadequate to decide on its relative merits. Paris green and sodium arsenate were used in the experiments, and the average amount of poison per hectare was 10–12 lb. The poison dust penetrated dense growths of reeds very well, and the dust remained on the leaves satisfactorily, especially if the dusting was done when there was a dew. The aeroplane, which was provided with a special dusting apparatus (see technical description by Korotkikh), flew very low, often touching the tops of the reeds.

The chief unfavourable feature of aeroplane-dusting seems to be the enormous waste of time and work involved in manœuvring the aeroplane, the actual number of hours of dusting representing only a small fraction of the total of flying hours. This becomes particularly unsatisfactory, when there are many small bands of locusts scattered over the area involved, as each band must be dusted individually ; dusting large areas is much more convenient, but this is seldom necessary in practice. The weather is also a very important factor in aeroplane-dusting, no work being possible when there is a wind.

An attempt has been made to cheapen such dusting by using diluted poisons and adding some neutral substance, such as lime, flour, or zinc oxide, but it was found that there was no difference in the amount of pure poison per unit of area required to obtain good results, while the weight of the dusting material to be carried increased five or six times, necessitating a greater number of landings for fresh supplies.

On the whole, it would be premature to give a final judgment on aeroplane-dusting for locust control, especially in view of the uncertain cost of the method. Certain points, however, are clear even now. It seems certain that this method cannot replace baits in the control of solitary grasshoppers in cultivated localities owing to the danger to man and domestic animals. In the case of locusts, aeroplane-dusting is only worth consideration in those countries where locusts breed in very large numbers and over large areas, since the larger the area to be dusted, the cheaper, relatively, becomes the dusting of it. Aeroplane-dusting may be of particular interest in cases where locusts breed in localities difficult of access as is the case with the Migratory Locust in reed beds ; in an open country, the use of aeroplanes can scarcely compare favourably with other methods such as baits and barriers. Of course, the future of the aeroplane method depends almost entirely on progress in the construction of small, easily and cheaply operated machines ; these may alter the position very considerably, and the above conclusions refer only to present-day conditions.

Poison Gases.—I will not discuss here the experiments with the war gases (chlorine) against locusts, made in Russia recently (Lebedev, 1922 ; Soldau, 1923), since they only showed that this method is enormously expensive and

very dangerous to the operators and to the population, while the results are uncertain.

On the other hand, there are very interesting possibilities in a method that has only recently been tested against locusts, namely, the use of calcium cyanide which generates cyanogas. Calcium cyanide is used in the form of a very fine powder, which under the influence of the moisture in the air produces cyanogas. The cyanide is simply dusted on the ground where a band or swarm of locusts is present, and the gas kills them through the respiratory organs. Experiments in Argentina on the South American locust are reported to have had very satisfactory results, bands of young hoppers being killed in about two hours. The action of the gas on older hoppers was less rapid and not certain under all conditions, particularly in windy weather. The best results were obtained when the bands were in dense and fairly tall vegetation, as this helps to increase the concentration of the gas, whereas indifferent results were obtained against the Moroccan Locust in Spain in very open places with but scanty vegetation (American Cyanide Company).

There are, of course, no definite data yet as to the cost of this method, but it cannot be very expensive, the more so as a dry mixture of cyanide with some neutral substance as a carrier might be tried.

While there is no information on the effectiveness and advantages of this method under different conditions. it may be suggested that it should be worth trying with regard to gregarious locusts, particularly the Migratory Locust in reed beds. On the other hand, there is every reason for doubting the practicability of applying the cyanogas method to the control of solitary grasshoppers or to locusts inhabiting dry open localities (Moroccan locust). In any case the idea on which this method is based seems a very sound one, and further research would be of great interest.

Agricultural Methods of Control

Some of the agricultural measures of control have been briefly mentioned already amongst the methods of destruction of egg-pods, and at present I propose to discuss, not the direct control of Acrididæ by agricultural methods, but only such measures as might prevent mass outbreaks. Exact experimental data bearing on this important subject are lacking, but there are a certain number of observations, which may serve as a basis for experimental work. These have already been quoted in the chapter on ecology as illustrations of the influence of certain agricultural methods on the ecological conditions that may be either favourable or harmful to Acrididæ. This means that it must certainly be theoretically possible to control Acrididæ by agricultural methods.

Speaking in a very general way, one might say that there is a certain connection between the general level of the agriculture in a country and the activities of Acrididæ. Countries, in which agriculture is only beginning to develop and the proportion of cultivated land is negligible in comparison with the virgin lands, do not suffer normally from Acrididæ, apart from exceptional

cases of invasions by swarming locusts ; the natural balance with regard to the non-swarming grasshoppers is not disturbed in such countries, and they can be entirely ignored. When the cultivated area increases, a twofold process takes place. On the one hand, the ACRIDIDÆ are forced to concentrate on gradually diminishing areas of uncultivated land owing to the tendency of the majority of species to lay their eggs in undisturbed soil. On the other hand, there are present large artificial areas of cultivated Graminaceæ, which, as we know, represent the favourite food of most ACRIDIDÆ. This stage in the agricultural development of a country is particularly favourable for the mass development of solitary grasshoppers, as may be observed, for instance, at present in Siberia, where the area of uncultivated lands serving as breeding-places for grasshoppers is sufficient to support a normal population, but it becomes too small during the increased multiplication of grasshoppers, and the latter then have to invade cultivated ground. The further agricultural progress of a country brings about a reduction of uncultivated areas to such an extent that their normal grasshopper population cannot become dangerous to cultivation even in years of mass outbreaks. This stage was reached long ago in Western European countries.

This broad principle applies, mainly, to solitary grasshoppers, but not to all species or everywhere. Thus, the solitary grasshoppers of North America have found exceptionally favourable conditions for their development in alfalfa culture. The latter at first was cultivated by very primitive methods, the soil of an alfalfa field remaining undisturbed for several years, and this, together with an abundance of good food, served as tremendous stimulus to a regular increase in the numbers of grasshoppers. When, later on, alfalfa culture began to be conducted more rationally, accompanied by disking and harrowing the soil, conditions became unfavourable to grasshoppers, and their numbers decreased again until they have now become dangerous only in years of heavy outbreaks. A similar case may be observed in Russian Turkestan, where there is a connection between alfalfa culture and the activities of *Calliptamus italicus*, though the problem there has not yet been studied.

These examples show, in a general way, that certain cultural methods or systems of agriculture may be either favourable or harmful to certain species of grasshoppers, and an outstanding problem in countries like Siberia is the study of each species of injurious ACRIDIDÆ with regard to local agricultural methods, *i.e.* to find out which cultural methods disturb the normal ecological balance and in what direction. In the solution of this problem with regard to the main grasshopper pests lies the only hope of agriculture in such countries, since, however effective control by poisoned baits may be, it must be applied almost continuously. Prevention of the increase in numbers of grasshoppers can be reached only by agricultural methods, and experimental work in that direction is most urgently wanted, but so far it is not being done anywhere.

In the case of the swarming locusts, the importance of the agricultural conditions of the country is still more pronounced. This is particularly well illustrated by the gradual retreat of the Migratory Locust (*Locusta migratoria*),

the breeding-places of which cease to function one after another. The history of the locust invasions in Europe abounds with instances of severe visitations by this species in the eighteenth and nineteenth centuries in Rumania and Hungary, and even in Austria and Germany, the main source of the invasions being traceable to large breeding areas in the delta of the Danube. During the same period, nearly the whole of Southern Russia was subject to periodic invasions by locusts breeding in the deltas of the Dnieper, Bug, Don, and Kuban. Towards the end of the nineteenth century, however, these invasions became rarer and rarer, until at present there is, of course, no locust problem in Western Europe, and Southern Russia is also free from swarms of this particular species. This means that the breeding grounds in the deltas of the rivers mentioned above have become unsuitable for breeding in large numbers. What, then, are the actual causes of this and what ecological changes in the breeding grounds are responsible for this change ? We can only put forward some theoretical suggestions, the exact data being wanting, though they would be of the utmost importance for the solution of the locust problem in other regions that still continue to suffer from locusts coming from other breeding areas. If we knew what ecological change in the Danube breeding grounds has made them inactive, we might be able to produce the same conditions artificially in the breeding areas of the Northern Caucasus or Turkestan without waiting, perhaps another half-century, for the change to come spontaneously. Direct control of the Migratory Locust in the breeding grounds is at present perfectly possible and very effective, but this work must go on, if only intermittently, for a very long period, unless methods of control of breeding grounds themselves are studied and applied.

An analogous case is presented by the Moroccan Locust, which breeds in fairly restricted areas in the hills of Mediterranean countries. These areas are not even sufficiently well defined apart from lack of exact knowledge of their ecological conditions. At the same time, there is no doubt that this locust is also dependent as regards its breeding on the agricultural conditions, but the exact method that might influence it unfavourably in its breeding grounds is a question that no one has ever attempted to solve.

Biological Methods

Utilisation of Parasites.—The question of utilising parasites for controlling Acrididæ has been raised in the literature more than once. Apart from the general suggestions of some older authors, the parasite method of control was advocated strongly by Portchinsky (1894). This author had especially great hopes of utilising the blister beetles. His observations during an outbreak of grasshoppers in the Ural region had led him to the conclusion that these parasites are often very unevenly distributed, and he suggested that the beetles may be collected where they are very abundant and transferred to other localities. A suggestion of this kind could be made only when wilfully ignoring the basic laws of ecology, since abundance of the beetles in one locality and their scarcity in another in the same country must be due to some natural causes

and not to an accident that can be easily remedied. There may, of course, be certain cases where a transportation of these beetles to the site of an outbreak of grasshoppers is possible, but the utility of this measure remains very questionable. Portchinsky quotes one example of this kind, when egg-pods of the Italian grasshopper in one locality were parasitised to the extent of 50 per cent., while in another, quite near by, there were no parasites at all ; even supposing that it were possible to distribute parasites more evenly, it is still difficult to see how it would affect the total number of grasshoppers destroyed by them.

A very important practical objection to the idea of utilising parasites is that plans of campaign cannot be based on a method, the success of which depends on a combination of unknown conditions ; this means that while using parasites the usual preparations for control must continue on the normal scale, and this makes the parasite method superfluous. Finally, the actual collection of masses of blister beetles in one locality and their transportation to another would be possible only in certain cases, such as when the two localities are reasonably near and do not differ greatly in their ecological conditions, etc. ; in other words, the campaign would have to be based on the use of an " insecticide " which might be either not available in time, or not transportable, or not effective. The necessity for effective control of an outbreak of locusts or grasshoppers is usually so serious that it would be criminal to base the campaign on such unreliable methods.

These or similar objections were apparently realised by Portchinsky himself, and in his later work on blister beetles (1914) he did not return to the question of their utilisation. He only there gives some perfectly sound observations on the rôle of these beetles as regulators of numbers of the pests, emphasises the importance of the quantitative analysis of egg-pods as regards parasites, and pays his tribute to sentimentality only in an appeal to agriculturists to " give a treat " to the beetles after they have done their useful work, it being well known that after an outbreak of grasshoppers the blister beetles bred on their eggs appear in large numbers and do serious damage to cultivated plants. From the point of view of the natural balance of grasshoppers and their parasites, the latter are bound to die out at such times, owing to the lack of food for their larvæ, however kindly they might be treated, and no farmer would look unconcernedly at his crops being devoured by blister beetles, while an entomologist recommending it would not be very popular. Destruction of beetles when grasshoppers are on the increase is never necessary, since the beetles appear in large numbers only when the curve of the increase of the grasshoppers is falling and the parasites have fulfilled their task for the time being.

Recently, Paoli (1920) returned to the utilisation of blister beetles for the control of the Moroccan Locust, and suggested the transportation of Algerian species of *Mylabris* into Italy. Since practically the same species of *Mylabris* parasitise this locust in the two countries, the project cannot be considered sound.

Other parasites that have been suggested for the control of Acrididæ are

larviparous flies. A very definite proposal of this kind was made in Argentina (Massini, 1917), but apparently without having been carried out even in the experimental stage. Still more recently, the problem was raised by Baranov (1924, 1925*a*) with regard to the Moroccan locust and the fly, *Blaesoxypha lineata*. Baranov has proved the practical possibility of the artificial culture of this parasite on living grasshoppers in the laboratory, and this enabled him to suggest continuous breeding of large quantities of the fly and the sending out of consignments of its puparia wherever they are wanted. He especially points out that it would be possible, when locusts exist in a given locality in small numbers only, to keep the numbers down by artificially bred and liberated parasites. Thus, he appears to reject the parasite method in the case of mass outbreaks, when it would be hardly practicable to breed enormous numbers of flies, for it must not be forgotten that they can be bred only on living ACRIDIDÆ. It seems, however, that even the utilisation of these flies for the maintenance of the number of locusts at a low level would not be very practicable ; in any case, there is no obvious advantage in this somewhat cumbersome method of reducing the numbers as compared with any other method (poisoning, etc.), which may be applied to the same effect and always with full confidence in the results, while the activities of parasites will always remain only partly controllable. I have purposely left out of consideration the doubtfulness of the utility of these flies, as controlling agents (see p. 123). The suggestion has been made that these larviparous flies should be introduced from one country into another (Berlese, 1916), but, since every country has its own species of these parasites, it is somewhat difficult to see the point of this proposal.

Utilisation of Birds.—The useful activities of locust-eating birds are so noticeable that there have existed in many countries from ancient times special laws protecting certain species of birds as man's allies in his war with locusts. In more recent times this problem attracted still more attention, and in South Africa, Egypt, and some other countries there is legislation in force, prohibiting the killing of certain locust-eating birds. This measure should certainly help in the maintenance of the natural balance of the numbers of locusts.

Certain enthusiastic lovers of birds, however, have not stopped at that, and they have advocated the employment of birds as a means of direct control of locusts. A project of this kind, for instance, has been recently advanced with regard to the Kalahari desert, where the Brown Locust was supposed to breed, and it was suggested that the desert should be artificially populated by certain species of locust-eating birds. Similar projects have been made in other countries, like Algeria and Transcaucasia. The theoretical absurdity and practical uselessness of these projects is obvious. Indeed, if a species of birds feeds mainly on locusts, the country cannot support more than a certain number of it ; when an outbreak of locusts occurs, their numbers increase at a very great rate, while the numbers of birds, of course, cannot increase so rapidly. Thus, the birds would be unable to check the incipient outbreak, and their utility would become of serious value only when the outbreak begins to abate.

A careful study of the birds feeding on locusts in each country and legislation to ensure their protection is all that can be done.

Mycological Method.—The striking effects of a natural epidemic of fungous diseases amongst ACRIDIDÆ could not fail to induce the idea of artificial dissemination of them as a method of direct control. Amongst the practical attempts of this kind that have been made in various countries, special mention should be made of the work in South Africa. About 1895 a fungous epidemic disease of locusts was very active in that country, and the local bacteriological institute undertook artificial cultivation of the fungus and distribution of its cultures amongst farmers. The results of its application were in some cases very good, in others negative. Requests for the cultures of the fungus arrived not only from local farmers but also from the government institutions of other countries anxious to test the mycological method. Examination of cultures received in this way showed, however, that they contained *Mucor*, a mould, not *Empusa grylli*, which is the true parasite of locusts. Experiments with cultures of *Mucor exitiosus*, received in this way in India (Butler and Lefroy, 1906), gave negative results—as might have been expected. Apparently, the initial natural epidemic was produced by *Empusa grylli*, but the artificial cultures were composed of *Mucor*, which was introduced accidentally; positive results obtained in some cases may be explained by natural outbreak of disease in the field. More recent careful studies of *Empusa grylli* have proved that it cannot be cultivated on any but living media (see p. 137).

The failure of the "South African Locust fungus," as it was called, of course does not exclude the theoretical possibility of using fungous diseases as a direct method of control. Skaife (1925) believes that the whole problem centres round the discovery of a suitable artificial medium on which *Empusa grylli* might be cultivated, and he thinks that such a medium can be found. In any case, however, there will always be a special drawback to the mycological method, namely, that the successful spreading of the epidemic is possible only when the weather if favourable, *viz.* damp and mild; this means that the whole campaign would be dependent on conditions beyond our control.

Bacterial Method.—d'Herelle, who in 1910 in Yucatan discovered *Coccobacillus acridiorum* causing a natural epidemic amongst *Schistocerca paranensis*, immediately attempted to use it in practice on a large scale. He found that the virulence of the bacillus can be increased by a series of passages through locusts to such a degree that swarms in the field can be infected by spraying vegetation with a culture, while the epidemic once started in that way would spread naturally to other swarms. The first reports of d'Herelle resulted in his being invited to Argentina for practical work of exterminating locusts, and, judging by his own account, he obtained remarkable results there. Whole swarms were reported to be exterminated within three days, and after a few days more, the epidemic spread over an area thirty miles in radius. These striking results were, however, not corroborated by a special commission appointed to check them. The commission, consisting of several bacteriologists, found that an epidemic cannot be produced in the field, that *Coccobacillus acridiorum* can be normally found in the intestine of healthy locusts, that it

has a mortal effect only when injected in the body cavity, and that infection through food, even in captivity, is impossible (Krause, 1916). d'Herelle himself in the meantime transferred his activities to Algeria, and obtained there again very good results in the field, which again were not corroborated by other specialists working there.

News of d'Herelle's discovery, which would make possible the destruction of locusts over vast areas within a few days and at a nominal expense, spread throughout the world and aroused enormous interest. Entomologists of all countries were from the first very cautious in their opinions as to the " new method," and this rendered them subject to vigorous attacks on the part of the press, and even from some bacteriologists and mycologists, who accused entomologists of being too conservative and too loth to part with " antiquated " methods of locust control in favour of the wonderful " new " method. In fact, however, entomologists were merely not taking any risks in attempting to apply the method in practice on a large scale, while they were studying it experimentally. Experiments of this kind were conducted almost in all countries interested in the problem, Algeria, Sudan, South Africa, Italy, Canada, Caucasus, Turkestan, and the Philippines. Almost everywhere the same results were obtained, namely, a good percentage of mortality could be obtained by direct injection of cultures into the body cavity, but field experiments either failed altogether or gave indefinite results. Apart from these experiments, which were sometimes conducted without reference to the most elementary rules of bacteriological technique, a series of more serious investigations were arranged by bacteriologists. The results of these investigations were still more unfavourable to the " new method." First of all, it was found that under the name *Coccobacillus acridiorum* a whole series of bacilli was being distributed, although the cultures were obtained from d'Herelle himself. Further, it has been proved that in all ACRIDIDÆ there are normal symbiotic bacilli that during the passages, which, according to d'Herelle, are necessary for the increase of the virulence, crowded out the original *Coccobacillus*, but are themselves pathogenic if injected into the body cavity. Barber and Jones (1915) experimenting in the Philippines even found that any bacillus, saprophytes included, may become pathogenic if its virulence is increased by a series of passages and if it is injected into the body cavity. This explains why various bacilli, distributed under the name of *C. acridiorum*, were found to be pathogenic when injected and yet ineffective in the field.

The fact that the " new method " disappeared from the horizon as quickly as it appeared, shows that it was absolutely unsound. If I have nevertheless dwelt on it, I have done so on purpose in order to show how easy it is to make brilliant " discoveries " and to advertise them, and how necessary it is for serious workers to maintain a critical attitude towards them until they are studied in detail.

The downfall of *Coccobacillus acridiorum*, of course, does not mean that bacterial diseases cannot be used for the control of locusts, but our almost absolute ignorance of these diseases makes it simply impossible to discuss the problem at present. Moreover, the problem of the artificial spread of bacterial

diseases cannot be as simple as it was made out to be by d'Herelle, who published very brief instructions for field work with his bacillus. Meteorological conditions must be of great importance in field work with bacterial diseases, and they cannot be controlled at will. Many years must be spent on the study of bacterial diseases of locusts before the time will come to return to the problem of their practical use. In this respect the " discovery " of d'Herelle had its uses, since it directed attention to this branch of the locust problem, while, on the other hand, its failure will be a good lesson to future investigators.

CHAPTER IX

ORGANISATION OF CONTROL

The technique of the control of the Acrididæ, discussed in the preceding chapter, has reached such a high degree of efficiency that from the technical point of view it must be regarded as one of the easiest problems of applied entomology, and the success of an anti-locust campaign can be always guaranteed on the sole condition that the campaign is properly organised. This is of supreme importance, since an absolutely perfect technique may be rendered useless or practically so by imperfect application. The problem at present is, therefore, mainly one of organisation, and in some cases even second-rate technical methods may give better results owing to good organisation, while cases have occurred of very indifferent results of applying the best methods owing to defective organisation.

The organisation of control measures differs greatly in the case of swarming locusts and of solitary grasshoppers, and these will therefore be discussed separately.

Organisation for the Control of Locusts

One of the fundamental characteristics of swarming locusts is, as we know, their habit of making extensive migrations; they cannot, therefore, be regarded as pests of importance only in the area actually invaded. Indeed, the areas adjoining the permanent breeding grounds are always under direct menace of invasion. The breeding areas themselves are, as a rule, situated in localities with a very low degree of agricultural development and often even uninhabited except by nomads. Such a population does not suffer from locusts, and the burden of their invasions is usually borne from year to year by the agricultural population of areas situated in the neighbourhood of the breeding areas. If locusts are regarded as pests of local importance, the population of these unfortunate areas should be called upon to control them and to bear in that way another additional burden. At the same time, the enormous depredations caused by locusts often reach such dimensions as to influence the crops of the whole country and the price of bread throughout it; in other words, the whole country is directly interested in the proper organisation of locust control, and remedial measures must not be left to local authorities or the population of the stricken areas; they should be at least supported and even directed by the central Government.

This point of view is, unfortunately, not recognised everywhere, or it is

recognised only partly. Thus, in South Africa, the existing laws provide only for the supply of materials and apparatus by the State, while the actual work of extermination of locusts is the duty of farmers ; in many other countries the State gives only technical advice, and the whole of the labour and the cost of control measures must be borne by the population of the areas affected. An exception to this occurs in Russia, where locusts are recognised by legislation as pests of exceptional importance and their control is the direct duty of the State ; this enables the latter to pursue a definite policy of concerted control of locusts in all breeding areas, and the advantages of such a scheme are too obvious to be discussed here. This arrangement in Russia has been brought about by the prolonged efforts of the entomologists concerned in the control of locusts, and the results attained speak for the soundness of the scheme. Whereas the disjointed and often half-hearted efforts of local organisations, unaided or but inadequately aided by the State, which is the practice in most other countries, cannot be expected to produce lasting results that are of value.

It is to be hoped that the principle of State interest and State responsibility in locust control will be fully realised in all countries concerned. This is the basis of a sound and wholly effective organisation of measures against locusts.

Basic Principles of Organisation of Control.—The first and most important principle of the organisation of control is the direction of the whole work by entomologists. This condition may seem superfluous, as it would be only natural that entomological work should be conducted by specialists in this branch, but unfortunately it is not generally recognised in practice. In most countries, even if there are entomologists at the head of the organisation, the actual work is being supervised and conducted by local administrative officers or by the staff of local agricultural departments ; entomologists, in most cases, are regarded as advisers only and are neither trusted with, nor directly responsible for, the execution of the control measures. This situation is brought about to a great extent by the mistaken policy of certain entomologists, who have deliberately evaded the heavy responsibilities connected with the direct organisation of control and have preferred the rôle of advisers. The results of this shifting of responsibility on to a technically incompetent personnel are almost invariably unsatisfactory, and this defect of organisation must be considered one of the main causes of the ineffectiveness of control measures in many countries. It is time to recognise clearly that the control of locusts is an entomological undertaking and that entomologists must be allowed to carry it out with full responsibility for the results.

It would, of course, be impracticable to build up the whole control organisation to the complete exclusion of administrative officers ; on the contrary, the latter should take a very active part in the work, but their function is only to assist the anti-locust organisation in obtaining the necessary labour, transport, etc.

The necessity for having entomologists in charge of anti-locust organisations is now recognised in most countries (though still not in all of them), but

this policy is not everywhere put into practice in the right way. In most cases there exist for this purpose special anti-locust organisations (South Africa, Argentina, Mexico), which are concerned exclusively with this work. While this is a very sound arrangement in the years of outbreaks, the system seems an unreasonable one in the intervening periods, when the organisation must be necessarily curtailed, involving the loss of some valuable workers. Moreover, an organisation that exists solely for locust control lays itself open to suspicion and attack from the general public on the ground that complete extermination of locusts would mean the end of the organisation and its disbandment. This can be avoided, and the general efficiency of the organisation considerably increased, if it is set up for the control of insect pests, including locusts. An organisation of this kind would be, no doubt, fully occupied even in the periods when locusts are at a minimum, while during the outbreaks it would need only a temporary increase of subordinate staff.

All the above remarks apply to the central organisation, which should be at the head of locust control, but the actual execution of the control measures must be also in the hands of a specially instructed technical personnel. This personnel is necessarily not permanent and is employed only during the actual anti-locust campaigns. The practice in most countries is to use for this purpose the services of local administrative or agricultural officers. This practice, while having certain advantages, is on the whole less convenient than the appointment of a special temporary personnel, directly responsible to the central control organisation. Indeed, only in this latter case can the smooth working of the whole machinery be attained, as it would be not easy for an entomologist to supervise and give orders to an administrative officer, perhaps of fairly high standing, who is accustomed to work independently. At the same time, the importance of the technical staff in the control work is very great, as the success of the campaign depends entirely on it. The members of this staff must be, therefore, well trained in the technique of control, but this alone is not sufficient, since they must not only know the methods of control, but must also understand them thoroughly so as to be able to apply them to the best advantage. They must know something of the bionomics of the locusts, since we know that the application, for instance, of poisoned baits requires the use of good judgment as to the time of the day when the baits should be scattered, etc.; in the case of work with barriers the technical staff must be thoroughly acquainted with the laws governing the movements of larval bands, or the whole work will be useless. All this requires not only purely technical training in the application of methods, but a certain degree of general intelligence and education, and members of the temporary technical staff must be recruited always with this point in view. Students of universities and agricultural colleges present particularly suitable material from which to recruit the temporary staff, since they are able to be trained quickly, to appreciate fully the necessity of adjusting control methods to suit the behaviour of the locusts, and to take an interest in the work. The temporary personnel may of course, be more cheaply obtained by selecting it from amongst persons of lower general education, but I must emphasise again that this personnel

is the backbone of the organisation, and it would be an unpardonable error to economise on it.

The next highly important point is the principle on which the workmen are recruited. In this respect I must insist that all labour employed in an anti-locust campaign should be paid for. This stipulation may seem unnecessary, but it is a fact that in nearly all the countries concerned the work of exterminating locusts is based on the employment of forced labour, the population of infested areas being obliged by law to take a direct part in the work. It is abundantly clear that such an arrangement is extremely unfair, since the population, which already suffers from the depredations of locusts, is compelled to abandon for several weeks all current agricultural work with results that are disastrous even to the crops that are saved from locusts. The sufferings of the populations thus obliged to combat locusts are well known to any one who knows the history of the locust problem, but in spite of this, laws to this effect are still in force in many countries. Particularly absurd is the position in countries where the population of breeding areas is not agricultural and, therefore, absolutely uninterested in the control of locusts, and this is the case practically everywhere. Apart, however, from the gross injustice caused by such laws and from the unavoidable exploitation of the population by unscrupulous lower-grade administrative officers, the results of the use of forced labour are always so inadequate that the practice has to be abandoned merely because this " free " labour costs the State too much in damages by locusts. Indeed, it would be hard to expect a peasant, obliged to leave his home and crops and to work, perhaps, in some other district, to be very keen on his job ; all he cares for is to serve his term of work and to return home, while there is no inducement for him to do his best ; if he is not working well, the officer in charge can do nothing but dismiss him, and there is nothing he would like better. A further disadvantage of using forced labour becomes particularly marked now that the present somewhat complicated methods of control are in use ; it is impossible to keep men away from their homes for the whole period of the campaign, and they usually take turns, with the result that as soon as one group is sufficiently trained in the technique of control, the men are dismissed and new and untrained ones replace them.

From the point of view of the State, the policy of using forced labour has also no justification. Indeed, the saving effected in this way is entirely fallacious, since one must put on the debit side, first, so many working days lost by the population, and, secondly, the enormous losses to the State caused by locusts as direct result of ineffective control. In fact, I do not know of a single case in the whole history of the locust problem when an invasion was speedily and effectively checked by forced labour. I do not hesitate to say that the employment of such labour must be regarded as one of the principal causes why the locust problem in many countries working on this principle remains permanent, and abolition of forced labour must constitute the first step towards effective organisation of control.

In some countries, in South Africa, for example, the organisation of control measures is based on a principle very similar to forced labour, peasants and

landowners generally being obliged by law to exterminate locusts on their land by any methods they choose, the Government giving them technical assistance in the shape of machinery, chemicals, and technical advisers. Special locust officers inspect the properties to see that the requirements of the law are carried out within a fixed period. The drawbacks of this scheme are obvious. First of all, each farmer is concerned only about his crops and, while destroying all swarms immediately threatening them, will not go out of his way to destroy also the swarms on the adjoining waste lands ; it is true that, by law, he is liable to penalties for this, but it is obviously impossible for a locust officer to survey his district in all details and not to miss any swarms, the more so that he cannot hope to obtain information as to the escaped swarms from the farmers. The results are easy to anticipate ; a certain number of swarms is bound to be overlooked, and these will give rise to a still greater number the next season. In this way, the work is extended almost indefinitely, and the invasion does not end except in its natural course of periodicity.

There are numerous objections to the system of fully paid labour in anti-locust campaigns, and the chief of these is the cost to the country, which, it is usually contended, would be beyond practical possibility. An analysis of figures of the relative cost of locust campaigns in South Africa and in Russia, where this system has been extensively used, shows, however, that it is very doubtful whether the system of using " free " labour is really cheaper. Indeed, the figures in a recent annual report from South Africa (Williams, 1926) show that the average cost of destruction of a swarm for the last three years was about eight shillings, this comprising all expenses (poison, transport, sprayers, and administration) except the labour supplied by the farmers. According to the official instructions to locust officers (South Africa, 1921), swarms of locusts should be classified as small if under 25 square yards, medium if under 1000 square yards, and large if over the latter figure. It would be, therefore, reasonable to suggest that the average figure for destroying a swarm applies to an area of 1000 square yards. Now, the average cost of spraying the same area in Russia, including all expenses of the campaign, works out about only sevenpence (at pre-war prices), or nearly one-fourteenth of the South African figure. Of course the cost of labour, transport, etc., in Russia is much cheaper than in South Africa, but even by doubling the cost to allow for the difference in prices, the South African figure remains seven times higher than the Russian. One reason for this is the enormous amount of poison used when spraying is done by the farmers, who are inclined to make the solution far stronger than is necessary. Indeed, from the same South African report we can calculate that as much as 0·6 gallon of undiluted poison was expended on each swarm ; this corresponds to 30 gallons of diluted poison for 1000 square yards ; in Russia the same area required, on the average, only 5 gallons.

This comparison, though admittedly far from being accurate, shows that work with paid labour may actually be far cheaper than with voluntary or forcibly recruited workers, owing to a much greater productiveness of work and the saving of waste of material.

A very effective substitute for paid labour may be found in some countries in the use of troops for the anti-locust work. This is done fairly often, but the practice may be extended with a great advantage ; of course, the technical side of the work should in this case, as always, be entirely in the hands of entomologists.

Summarising the above, I will repeat that the two main principles of successful organisation of control are (*a*) centralisation of work in the hands of specialists, and (*b*) the use of paid labour. The following discussion of details of organisation is based on the assumption that these conditions are fulfilled.

The Course of a Campaign.—Amongst the general public, in administrative circles and partly even amongst specialists, the view is very commonly held that locust invasions are a kind of cosmic catastrophe and that the measures against them must be planned accordingly, *i.e.* without reckoning the cost and by throwing into the struggle all available resources. This point of view is both erroneous and harmful. The present-day technique of locust control is so highly efficient that entomologists are able to undertake the work on any scale with a complete guarantee of success. The times of heroic wars against locusts when the whole population turned out to dig miles of trenches, to kill locusts with brooms, and generally to do useless work on a gigantic scale are past ; at present the problem is reduced to the mass poisoning of the insects, and this must be done, not only effectively, but also cheaply. This can be attained only if the campaign is based on an exact knowledge of the amount of work to be done, which would enable those in charge to estimate the amount of materials, machinery, and labour required. Estimates of this kind can be based only on the sum total of the areas that are to be treated, and therefore, a survey and estimate of the size of the areas infested must be considered the fundamental step in the campaign. The importance of this survey is not realised in most countries, but in Russia it has been in practice for many years, and the results are eminently satisfactory.

The *survey of infested areas* must begin during the period of oviposition by flying swarms. It has two main objects : first, to discover all the localities where it will be necessary to conduct the work of extermination, and, secondly, to determine the size of the areas infested in order to be able to prepare estimates for the campaign. The first of these two tasks is of enormous importance for the future campaign, as it enables the officers in charge to plan the distribution of staff and materials beforehand, and it makes impossible unpleasant surprises in the shape of the unexpected appearance of locusts where no preparations have been made to deal with them. It is clear, therefore, that the greatest attention must be paid to this part of the work. This is done by a specially trained staff, members of which are distributed over all districts where flying swarms are present, or may be expected. Each of these surveyors has to watch his district for swarms, keep each of them under observation, and take a note of the exact places where eggs are deposited. Since it is usually impossible for one man to keep under direct observation a large district, assistance from the local administration and from the population

must be obtained ; this assistance consists in notification of surveyors (by telegraph) of all swarms that appear, the direction of their flight, their halts for oviposition, etc. All this information must be immediately checked by one of the members of the surveying party

The actual survey work is done in this way. The first indication of the places where the eggs may be found is offered by observations on flying swarms and their stopping places ; all places where a swarm has passed more than one day must be regarded as possibly infested and must be investigated by digging for egg-pods. Absolutely necessary to the surveyors is a knowledge of the ecological conditions under which the species of locusts in question usually lays its eggs ; thus, the eggs of the Moroccan locust should be looked for only in hard uncultivated soils, etc. There are, further, certain subsidiary observations that make the detection of egg deposits relatively easy. Thus, certain birds (rooks, storks) congregate in numbers to feed on locust eggs, and the sites of oviposition may be found in this way ; even when the birds have left, the surface of soil disturbed by their digging for eggs attracts attention. In many cases locusts die off soon after oviposition, and an accumulation of dead locusts is often a useful indication that the eggs are there, or not far away. Every suspicious place must be examined by means of trial excavations, and the surveyor must be familiar with the egg-pods of the particular locust and must know at what depth they are laid. If any eggs are discovered, the area infested must be determined. In order to do this test diggings are made in all directions outwardly from the first one until no eggs are found. The edges of the deposit are indicated by small mounds of earth, heaps of stones, or other marks that will last until the beginning of the campaign. When the shape of the deposit is determined in this way its area may be calculated, and the deposit marked on the map. It is not necessary to do this work very exactly ; the shape of the deposit does not matter during the control work, and the area should be estimated only approximately in order to help with the estimates for the campaign.

Apart from the size of the infested areas and their position, surveyors ought to find out the degree of infestation ; this is determined by test excavations of a definite area and is expressed in terms of so many egg-pods to a square foot or metre. The degree of infestation of egg-pods by parasites should be also noted, as in some cases the eggs may be so heavily parasitised that no control measures will be necessary. Further data necessary for the estimates are distances of deposits from habitations, roads, and the nearest water ; remarks on the presence and site of cultivation near the deposit may be also very useful when the plans of campaign are being drawn.

All the data on deposits are then summarised by districts and for the whole area, and the plans of campaign and estimates can then be drawn up on this basis.

Plans and Estimates for the Campaign.—The first question to be settled when preparing the plans of a campaign is, of course, the method of control that is to be used. At the present time, the selection is restricted to poison baits, barriers, and, perhaps, dusting with aeroplanes. Since the latter method,

however, is still in its infancy, and barriers may be recommended mainly as a supplementary method applicable only in certain cases, we will assume that the campaign will be conducted by means of poison baits.

Estimates must be based on the area that has to be poisoned. This is not exactly the same area as that infested by eggs, since young hoppers segregate in dense bands and occupy less space than the eggs from which they have hatched. Some entomologists maintain that the estimates should be made on the assumption that the whole area of egg deposits will have to be poisoned ; others believe that only a certain part of the area should be taken into account. The first view is more popular, since it permits those in charge of the campaign to be on the safe side in case of some areas of egg-deposits having been overlooked. This, however, should not happen if the survey has been properly organised, and the deliberate inflation of estimates indicates only that the person in charge is not certain of success ; a really good entomologist should be able to estimate the danger exactly and to make preparations to meet it with only a small margin for unexpected developments.

It would be difficult to state definitely what fraction of the infested area should be taken as a basis for the estimate, because the poison-bait method is relatively recent and there are no exact figures from any extensive campaigns. Such figures for spraying, however, were obtained in my campaigns in the Northern Caucasus, and there it was found that the estimates may be made on the assumption that about one-half of the infested areas will have to be poisoned ; it seems reasonable that the same applies to poison baits.

The figures obtained from previous campaigns ought to show the average amount of materials (carrier, poison) and of labour necessary to poison a unit of area. Based on these, the amount of materials and the cost of labour for the whole campaign may be estimated.

The estimates, then, must be completed by the addition of the costs of the technical staff, transportation of materials, and other general expenses.

The plan of the campaign is prepared when all maps of the infested areas are ready. I would emphasise, however, that it is absolutely necessary for the entomologists in charge to have a first-hand personal knowledge of the infested districts and not to rely on maps only. This is particularly important for the most practical division of the whole area into separate districts which will be under direct leadership of district locust officers. It is not necessary that the division should correspond to administrative units, but it must be done solely as is most convenient for the conduct of the campaign. If the campaign has to be conducted over the whole of a large country, further subdivision may be necessary ; in any case either the entomologist in charge or the district officers must be able to supervise the campaign personally.

Side by side with the division of the area into districts must go the establishment of local depôts in each district for the storage of materials, and when these have been distributed to the respective depôts, the preparations for the campaign may be considered complete.

The Control Campaign.—District locust officers and other technical staff must be at their respective posts at least a fortnight before the suggested

beginning of the actual work in order to be able to study the locality and all its conditions, as well as to check once more the egg deposits. This latter work is necessary especially with regard to the infestation of egg-pods with parasites, since the results of the activity of certain parasites (Bombyliids) become apparent only shortly before hatching time.

Observations on the hatching are then instituted in order to determine the exact date when the extermination work should be started. This depends to some extent on the method of control used ; if the work is done by poison baits, their application at too early a stage would be practically useless (see p. 76), and the work should start when the hoppers have reached the end of the first stage. In the case of barriers, it is of some advantage to delay the beginning of the work a little more until larger bands are formed and their movements became more regular. Though unnecessary delay at the beginning of the work must be avoided, as it tends to increase the nervousness of the population, too early a beginning has still another disadvantage in that all the eggs in a given deposit do not hatch at once and the period of hatching may extend over a week or even more ; if the work has been begun too soon, it will have to be repeated in order to exterminate the hoppers that have hatched later.

The fundamental rule of control work is to keep cool and refuse to be rushed by farmers, who usually get very nervous when the danger is still far from their fields. The technical officers in charge of working parties must know exactly what they can do and, above all, be able to grasp the continuously changing situation and act accordingly ; on their initiative depends almost entirely the success of the campaign.

The part played in the campaign by the entomologist in charge depends on the extent of it. If the latter is conducted over a restricted area which may be covered without loss of time, he must travel from place to place and supervise the campaign personally. If, however, he has to conduct a campaign over the whole country, it is better that he should remain at headquarters directing the campaign by telegraph and telephone, and the actual supervision of the work should be delegated to district officers or assistant entomologists. In any case, these supervising officers must have the means of rapid transport over the respective areas so as to enable them to visit every working party several times during the campaign, and to see for themselves the progress of work instead of relying on the reports of their technical staff. The problem of the transport of such officers is a very important one and must not be forgotten when estimates are prepared ; motor-cars and even aeroplanes (in the case of very extensive campaigns) would be of the greatest value and always justify the expense. Field telephones and wireless for continuous communication with all working parties are also very useful.

A campaign against locusts must always have as its aim a complete *extermination of all the swarms* in the area, not merely the defence of cultivated fields from damage. This can be done only with the aid of a properly organised and effective *scouting service*. For this purpose it is useful in populated areas to offer a reward for every swarm reported and not previously known to the working party ; in thinly populated, or desert, areas, special scouts must be

attached to each party. Usually the scouts are mounted, and their duty is to find and mark (by flags) all bands ; they work mainly in the evenings and early mornings when hoppers are on the plants and the bands are clearly visible from afar. Aeroplanes can be of enormous help in scouting (Sviridenko, 1926), but their high cost makes their use practicable only in certain cases.

Since locusts lose their swarming habits when the bands are scattered, it is not necessary to exterminate all the hoppers completely ; it is quite sufficient to destroy all bands, including small ones.

The time when the work must be terminated depends on the degree of success attained. If all bands can be destroyed, the campaign can be terminated gradually by reducing the number of working parties in proportion to that of the bands that still remain. If, however, for some reason the campaign has not been entirely successful and some bands escape extermination, the work must go on at full speed until the last moment. This moment is usually defined by the hoppers acquiring wings, but recent practice shows that it is possible to use poison baits with good results even for adult locusts, at least for some time after they become winged. If some flying swarms still remain, observations on their movements must be instituted immediately on the completion of the campaign.

Reports of the Campaign.—The great majority of reports on locust campaigns in various countries suffer from overloading with data of purely historical interest, describing the course of the work in different districts, movements of working parties, etc. All these data cannot possibly be of any use in the future and could safely be left unpublished. On the other hand, there is always a remarkable lack of useful figures which might help in preparations for future campaigns both in the same country and elsewhere. Sometimes we find in reports figures such as the numbers of swarms destroyed or even the weight of the locusts exterminated, but these are obviously intended to impress the authorities and the general public and are useless in other respects. What is really wanted are exact figures reflecting the effectiveness of each method and each variety of the methods employed, as well as what they have cost in materials, labour, etc.

When working with poison baits, it is necessary therefore to keep exact returns of the poison and carrier used and of the labour employed. Sometimes these figures are recorded in connection with the area poisoned which is determined by approximate measurements, but this does not seem absolutely necessary and may even lead to serious mistakes in final calculations, because some heads of working parties are apt to try and exaggerate the amount of work done by returning larger figures of the area poisoned than was actually the case. It is better to make several empirical determinations of the area that can be poisoned with a given quantity of poison bait and then record only the bait used, deducting afterwards the area from the total expenditure of the bait. To make this method more accurate, determinations of area per unit quantity of bait must be done repeatedly and under actual working conditions ; to ensure this, it may be made the duty of heads of working parties to make one determination each day and to put the results down in his diary. The diary

may be of somewhat varying form, according to local requirements, and it would be useless to describe here a standard pattern for it, but any such diary must give exact answers to the following questions : quantity of carrier and of poison used during the day, number of workmen, and area covered ; there may be, of course, additional remarks on the conditions of work, etc. The most important point in keeping such diaries is to record separately the work done by each variety of poison bait and under different conditions. If, for instance, the work has been done partly by a bait of bran and arsenic, and partly by bran with sawdust and Paris green, it would be absurd to enter the data together, as they will then be valueless for comparing the cost and effectiveness of the two mixtures. Similarly, if the work covered areas of widely varying conditions, as, for instance, dense crops and semi-desert, it is imperative to keep the records apart, in order to be able to appreciate the cost and effectiveness of the method under different conditions. All this seems very obvious, but, unfortunately, there are too many printed reports on locust control, *e.g.* by spraying, based on average figures for spraying tall reeds and very short grass, and they are clearly useless.

General Policy of Locust Control in One Country. — In the preceding paragraphs I have given a brief outline of how an anti-locust campaign should be prepared and conducted. However effectively campaigns of this kind might be conducted, they cannot attain permanent results and can only aim at the defence of the year's harvest and at a speeding up of the period of minimum of locust activity, which will be inevitably followed in due time by another increase and finally another outbreak, requiring new campaigns. This is exactly what we may see in all countries subjected to locust infestation, where extensive locust campaigns follow one another at intervals, but without any end in sight. Governments and the general public lay the blame for it on entomologists who appear to be unable to " exterminate " locusts, and the solution of the problem is sought in improvements of technique of control, whereas the root of the problem is defective organisation. Indeed, the usual course of events is as follows. The initial increase in the numbers of locusts in their normal breeding grounds usually remains unobserved, since there is no organisation that keeps the breeding areas under continuous observation. This is followed by a further increase, which results in the formation of a swarming phase ; then some swarms emigrate and invade cultivated districts. It is at this stage, and not earlier, that hasty preparations to meet the " unexpected " invasion begin, but the first season's campaign is rarely a complete success because of tardy preparations. This gives a chance to the locusts, which are just entering the most active stage of their development, to form larger swarms, and a general calamity is the result. Official recognition of the seriousness of the situation always comes too late, and only by the time that the inevitable decline in locust activities sets in and a transformation into solitary phase is in progress, is the organisation of control perfected and the invasion suppressed. During the following period of locust minimum, all previous lessons are forgotten, and the whole story repeats itself in a few years.

It is clear that, in order to attain more permanent results and not to spend

enormous sums of money on locust control, a country must follow a definite and far-sighted policy. This must be not merely defensive, but offensive, the aim being not only to reduce damage to crops, but to anticipate the possibility of it. This aim can be attained if the control measures are concentrated on breeding grounds and locusts are never allowed to increase in them and to transform into the swarming phase. The ideal, but not easily attainable, situation would be reached by artificially altering the ecological conditions of breeding grounds so as to make them unsuitable for the locust in question (see p. 196) ; this is, however, out of the question at present for the majority of locusts, and attention must be turned to the control of locusts in the breeding grounds which function as such.

To ensure a perfect control of locusts in their breeding grounds, the latter must be kept under permanent observation by a specially trained staff, which surveys the grounds thoroughly during the period from the appearance of hoppers and until oviposition in order to estimate the situation and to find out whether there is any tendency to swarming. This work is highly responsible and must be under the direct control of an entomologist well acquainted with the locust in question, its bionomics, phases, etc. If a tendency to swarming is observed, the incipient small bands of hoppers must be immediately poisoned ; it would be sufficient in this case simply to thin out the bands, as that would stop transformation into the swarming phase (see p. 157).

The cost of such organisation of control in the breeding areas cannot be very great, while the advantages derived from it are too obvious to be discussed in full ; they would result in enormous savings since there would be no emigration of swarms from the breeding areas, no damage to crops, and no need for organising anti-locust campaigns on a large scale. Incidentally, the same entomologists would be able to achieve a great deal in the direction of ecological studies on the locust, and thus approach the solution of the problem of altering the breeding places with a view to making them unsuitable for the swarming phase of the species.

The first obvious step towards the only rational organisation of control is, therefore, a study of the breeding areas of the local species of locust. Unfortunately, very little attention has been paid so far to this question anywhere, and we are still in ignorance as to the breeding areas of most species of locusts, or these areas are so vaguely defined that no practical use can be made of the information.

The International Aspect of Locust Control.—The view is often expressed that definite success in locust control can be reached only if it is done on an international scale, and special international conferences have even been organised with this aim. The first conference of this kind, which took place in Rome in 1920 (Institut International d'Agriculture, 1916, 1921, 1926), arrived at the decision that it was necessary to form a convention of States interested in locust control, the States joining the convention accepting an obligation to control locusts by the best available means. The convention was actually signed by several States, but it must be admitted that the idea is very far from being practical. Indeed, it can hardly concern, for instance,

Argentina that locust control should be organised properly in Morocco and *vice versa*, so that a really world-wide anti-locust convention is not actually justified. At the same time, in certain cases something must be done to ensure co-operation in locust control between countries, and this applies to the cases when a natural area of distribution of one species of locust covers more than one adjacent country. Situations of this kind exist, for instance, in the South American Republics (*Schistocerca paranensis*), in the French and Spanish possessions in North Africa (*Schistocerca gregaria*), in Transcaucasia and Persia (*Dociostaurus maroccanus*), etc. In such cases a close co-operation between the countries concerned becomes imperative. It would be difficult to outline what form this co-operation should take in practice, since it depends on various local conditions. In some cases, when a proper organisation for control exists only in one of the two countries (Transcaucasia and Persia, for instance), it may be found advantageous for the more advanced country simply to send its working parties into the other in order to destroy the source of a possible invasion. When, however, control is organised in both or all the countries concerned, a close contact should be maintained between their respective anti-locust organisations, both in planning campaigns and in conducting them. Such co-operation may be best secured by special conventions, providing for periodic conferences of entomologists and other officials immediately concerned in locust control. I should like to emphasise this point, since it is very often the practice to appoint to conferences of this kind, as representatives of countries, diplomats and other persons of high official standing, but with very vague ideas on the problem under discussion.

Apart from these cases, each of which can be dealt with separately, there is not much scope for a really world-wide anti-locust convention. It is sometimes suggested that international conferences of this kind might result in finding out the best technical means of control, but all phases of technical progress are always duly reflected in the entomological literature, in reports on anti-locust campaigns, etc. Thus, international conferences cannot be of practical use, either from the point of view of organisation or for the advancement of the technique of control, and these are the only two points that have been so far subjects of conferences. On the other hand, the scientific side of the locust problem has been entirely ignored by such conferences, while enormous advantage might be derived in this respect by action on an international scale. We have seen in the preceding chapters how a study of certain aspects of the locust bionomics in one country was supplemented by the results obtained elsewhere, and also how proper organisation of control is handicapped by the very imperfect state of our knowledge of bionomics. The crucial point of the locust problem is the question of periodicity and its causes ; some results in this direction have been obtained by independent workers in Russia, South Africa, the Sudan, and elsewhere, but in all cases they were obtained quite casually and partly by entomologists working semi-officially. In no country is there at present a properly equipped laboratory for the study of the locust problem in all its branches, and even if such existed, it is not always possible to solve all the problems involved in any one country. In this I see the real opportunity

for international co-operation in locust control, and efforts in this direction would be of the greatest benefit to all countries suffering from locusts. In practice, it would be necessary to inaugurate research work on the bionomics and control of locusts on an international scale by establishing a central research institution connecting and assisting research carried out in various countries. In this way, preliminary results obtained in one country could be immediately tested and verified elsewhere, and the solution of many problems of general importance could be attained more speedily than in any other way. I do not think it necessary to elaborate the scheme here, as I am afraid that there is very little likelihood of its being carried out within our time, but I am sure that it is the only correct policy for the international control of locusts.

Organisation for Control of Grasshoppers

Fundamental biological differences between locusts and non-migrating grasshoppers make the organisation of control outlined above for the former, both unnecessary and impracticable for the latter. Grasshoppers, even in the years of mass outbreaks, remain pests of purely local importance, and do not constitute a direct menace to neighbouring districts ; consequently there is no absolute necessity for a simultaneous and uniformly organised campaign throughout the area infested. The general economic interests of the country may of course require an organisation of a grasshopper campaign on a large scale, but the principles of organisation need not be the same as for locusts. Indeed, there are no definite and relatively restricted breeding grounds for grasshoppers, and they usually breed over very large areas ; to attempt a centralised organisation, with paid labour, for their control would be too expensive and not justifiable. On the other hand, it is perfectly practicable and very advantageous to base their control on the active co-operation of the agricultural population, since the grasshopper problem usually arises only in areas of relatively dense cultivation. The poison-bait method, being exceedingly simple and very effective, is the only one that can be used in these campaigns, and, as a matter of fact, they can be properly organised only when this method is applied.

As in the case of locusts, all preparations for a grasshopper campaign must be in the hands of entomologists, and they should be responsible for the technical side of the campaign itself, while general administrative officers should only assist them in their work. On the other hand, more scope than in the case of locusts should be given to local agricultural officers, since they have a special qualification for the work at hand in their personal knowledge of farmers and peasants who are to take part in the campaign.

The survey of egg deposits in the case of grasshoppers cannot and need not be as detailed as for locusts. For practical purposes it would be sufficient to obtain approximate data on the area infested in each district in order to organise district depôts for poison for distribution. The carriers for baits should be prepared by farmers and peasants themselves in quantities sufficient for poisoning grasshoppers on their own land. To induce them to do so,

meetings and lectures are organised throughout the area long before the campaign is due to start, and full instructions for control are issued and freely distributed.

Shortly before the beginning of the campaign, all the technical staff should be distributed over the area, on a definite plan, each member of the staff being given one or several villages or communities where he has to organise the work. While it is possible to obtain fairly satisfactory results by simply inducing each farmer to poison grasshoppers on his own land, it is much more desirable to organise the work on a community basis, so that all lands in the district would be cleared from grasshoppers and there will be no danger of them surviving for the next season.

There is very little to be said about the organisation of the control work itself, since it depends greatly on local conditions, which the entomologist must be able to utilise to the best advantage. When the work of scattering baits is done individually by each farmer on his own land, nothing is required from the entomologist beyond supplying poison and technical advice, but for community work, special poisoning parties should be formed. These may consist of five to six men each, one of them with a horse and cart. The party is assigned (by the entomologist) to an area where it should work, and a base is formed. At the base two men prepare the bait in two boxes ; while they fill one box, three other men scatter the bait from the second and then change it for the other ; the work thus goes on without interruption (Berezhkov, 1923).

If the work is carried on on a very large scale, it may be practicable to establish a central mixing centre where the bait would be prepared by machinery (see p. 190) and transported to the scattering parties. The work is usually organised in the United States in this way.

As regards the general policy of grasshopper control, continuous observations on the balance of the insects in the areas liable to outbreaks are obviously necessary, but they can be effectively carried out by local entomological organisations, and there is no need for special surveys. The importance of suppressing an outbreak as soon as the numbers of grasshoppers begin to show an increase is obvious, but in practice it will be found hardly possible, since it is very difficult to induce farmers to start work when there is no direct menace to crops. International organisation, except in respect of research, is quite useless in the case of grasshoppers.

SPECIAL PART

CHAPTER X

THE MOROCCAN LOCUST (Dociostaurus maroccanus, Thnb.) AND THE LOCUST PROBLEM IN SPAIN, ANATOLIA, TRANSCAUCASIA, AND TURKESTAN

Description of Stages

Adult Insect (Fig. 82).—Pale greyish-brown, with dark spots. Antennæ long, fine. Foveolæ of vertex trapeze-shaped, narrowed forward. Frontal ridge in the female flat, in the male with a shallow depression above the median ocellus. Pronotum constricted in the middle; its hind transverse furrow placed in front of the middle; the hind part (behind the furrow) of a dark colour, included between sharply defined whitish oblique stripes, forming an X-shaped design; lateral lobes of pronotum each with a small pale spot in the middle. Elytra extend beyond the hind knees (in the solitary form only reaching them), practically transparent, with not large dark grey spots. Front femora thickened, especially in the male. Hind femora above with three sharp, blackish spots and black knees. Hind tibiæ red, at the base grey. Subgenital plate of the male (Fig. 82, S) with the apex truncate (this latter character serves best to separate the species from others of the same genus that are very similar).

Length of body, male 20–28 mm., female 22–33 mm.; elytra, male 20–27 mm., female 25–36 mm.; hind femur, male 15 mm., female 20 mm.

Egg-pod (Fig. 42, M).—Shape of egg-pods very variable; straight cylindrical, or slightly bent, or strongly bow-shaped, sometimes even bent at an angle, which depends probably on the character of the soil and on the obstacles (stones, etc.) met by the ovipositor of the female when digging a hole for the eggs. As the typical form, may be taken a slightly bent cylindrical egg-pod, somewhat widened towards the lower end, which is rounded.

The walls of the pod are very hard and thick, consisting of earthy particles cemented together by the secretion of special glands; small stones and bits of roots of plants are often embedded in the walls. The firmness of the walls is remarkable and ensures preservation of pods in the soil for a very long time; Büchner (1918) records a case when some old pits full of empty egg-pods were found in Anatolia in 1916; these pits had been made about forty years before to bury egg-pods collected by the population. This character of the egg-pods of the Moroccan Locust is important from the point of view of surveying egg-deposits, as an inexperienced surveyor may easily mistake old and empty pods for fresh ones.

The walls of the inner cavity of the pod are lined with a membrane that is as thin as paper; the membrane is the hardened secretion of certain glands, and

it can be separated from the walls if the pods are placed in water. From one- to two-thirds of the upper part of the cavity are filled with a yellowish, shining, porous substance, while the eggs occupy the lower part.

The number of eggs in a pod varies from 18 to 40, the average being 30–35. The eggs are placed in four rows, somewhat obliquely to the longitudinal axis of the pod.

The egg is elongate-cylindrical, somewhat curved, with the ends rounded. Its colour is whitish-yellow, the chorion, which peels off very easily, being of this colour; the outer surface of the chorion, according to Plotnikov (1926), has no particular sculpture, but La Baume (1918) describes it as provided with

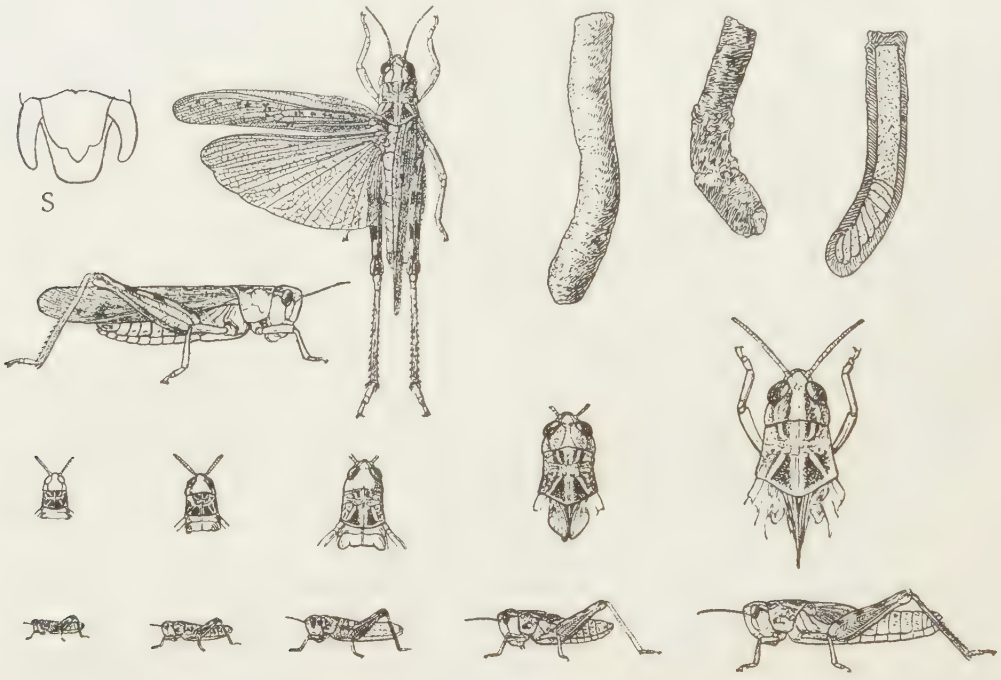

Fig. 82.—Moroccan Locust. Two females, egg-pods, hoppers of all stages, natural size (after Plotnikov). S, end of the male abdomen, enlarged (after Künckel).

raised ridges visible under the microscope. The eggs in recently laid pods are about 5 mm. long and 1–1·2 mm. in diameter; before hatching the length is 5–6 mm., and the diameter 1·5–2 mm. The weight of an egg is 9·5–12·5 mgr.

The upper end of the pod is covered by a lid, which is as hard as the walls, and is separated from them by a slightly thinner ring, which makes it possible for the hatching larvæ to lift the lid (Fig. 29).

Hoppers of the First Stage.—Antennæ 13-jointed. No distinct rudiments of elytra or wings. Hind margin of pronotum slightly excised in the middle. The lower hind corners of the mesonotum and metanotum are right-angled, with the apex rounded.

General coloration brownish-black. Pronotum with a fairly distinct

yellowish X-shaped pattern, interrupted in the middle; within the pattern the pronotum is velvety-black, darker in the hind portion; lateral lobes with a black central spot. Along the upper side of the head, pronotum, and abdomen there sometimes runs a narrow white, or a broader yellow, median stripe. Abdomen yellowish-brown, with black dots and irregular spots. Hind femora yellowish-brown with three blackish-brown fasciæ, and the knees of the same colour. Hind tibiæ black, with a pale ring near the base.

Sexual characters feebly pronounced; in the female the eighth and ninth sternites look like small plates with depressions in the middle; in the male there are no such depressions.

Length at the beginning of the stage 5 mm., at the end 8 mm.; hind femur 3–4 mm., antennæ 2 mm. (Increase in the length of body towards the end of the stage is due to stretching of the abdomen.)

Hopper of the Second Stage.—Antennæ 15–17-jointed. Lower hind angles of mesonotum and metanotum somewhat acute and attenuate backwards, forming rudiments of elytra and wings. Hind margin of pronotum practically straight.

The coloration becomes more vivid and often has a reddish tint. X-shaped pattern on the pronotum becomes sharper, and the velvety-black parts of the pronotum deeper in shade.

In the female two pairs of pointed rudiments of the ovipositor can be seen; in the male there is one protruding plate, the rudiment of the subgenital plate.

Length at the beginning of the stage 6·5 mm., at the end 11 mm.; hind femur 4–5 mm.; antennæ 2·2–2·6 mm.

Hopper of the Third Stage.—Antennæ 20-jointed. Lower hind angles of mesonotum and metanotum forming distinct rudiments of elytra and wings with raised longitudinal ridges (veins); rudiments of elytra (on mesonotum) considerably shorter than rudiments of wings (on metanotum). Pronotum behind almost covering the mesonotum.

Coloration still more vivid, and on the cheeks and pronotum appear some orange-yellow spots. Black spot on the lateral pronotal lobes very distinct. Rudiments of elytra and wings become black.

The female can be easily distinguished from the male by the clearly visible valves of the ovipositor.

Length at the beginning of the stage 8 mm., at the end 14 mm.; hind femur 6–7 mm.; antennæ 3·2–3·6 mm.; elytral rudiments 0·5 mm.; wing rudiments 1·3 mm.

Hopper of the Fourth Stage.—Antennæ 21–22-jointed. The shape and the position of elytral and wing rudiments change considerably; elytral rudiments are now elongate, narrow, and covered by the triangular wing rudiments, which are much longer than they are; both are turned round their longitudinal axis and directed not downwards, as before, but upwards, and on the back the rudiments of the two opposite sides practically touch each other.

In coloration and pattern there is little difference from the preceding stage, but the general tint becomes paler, with the orange-yellow parts more distinct; cheeks become orange-yellow. Elytral and wing rudiments black.

Length at the beginning of the stage, male 13 mm., female 15·5 mm. ; at the end, male 19 mm., female 21 mm. ; hind femur 8·5–9·2 mm. ; antennæ 4·5–5 mm. ; elytra 3 mm. ; wings 3 mm.

Hopper of the Fifth Stage.—Antennæ 23–24-jointed. Elytral and wing rudiments in the same position as before, but they have increased in size and now cover the abdomen nearly or quite to the middle ; their veins are very distinct. Hind margin of pronotum angulate.

Coloration becomes paler. Black spots of the pronotum stand out very sharply against reddish-yellow background. Wing rudiments black, with a kidney-shaped pale spot near the base.

Length at the beginning of the stage, male 17 mm., female 19 mm. ; at the end, male 24 mm., female 28 mm. ; antennæ 6–7 mm. ; hind femur, male 13 mm., female 10·5 mm. ; wings, male 7·5 mm., female 8·5 mm.

Distribution and Ecology

The area of distribution of the Moroccan Locust comprises dry, mountainous, or at least hilly regions of Mediterranean countries in the wide sense of the word (Fig. 83).

The extreme south-western outposts of this species are in the Canary Islands, where it seems to be always common and in certain years appears in large numbers causing heavy damage. There are no data on the ecological conditions under which the species lives in these islands.

An important permanent breeding ground of the Moroccan Locust lies in the Atlas mountains, in Morocco, Algeria, and Tunisia. There is, apparently, a chain of breeding grounds stretching from the Atlantic coast of North Africa to the Gulf of Gabes on the Mediterranean, but unfortunately no one has ever attempted to study these grounds even from the point of view of their location, and ecological data on them are, of course, non-existent. Künckel, it is true, studied the locust problem in Algeria for several years, but he published only an enormously voluminous historical survey and some observations on certain problems of bionomics of the local locusts, mainly on their parasites. As regards the distribution of the Moroccan Locust in Algeria, he merely remarks that the species breeds in the Atlas mountains on uncultivated, often stony, slopes, and that in the years of mass outbreaks its swarms invade neighbouring plateaus with a steppe type of vegetation, where temporary breeding grounds can develop. Further migrating swarms may invade the cultivated plains, but the species cannot breed there. This seems likely, but more detailed information is necessary.

In Spain and Portugal the Moroccan Locust is almost a chronic pest. In spite of this, the data on its distribution there are very unsatisfactory, being represented only by the information contained in the official reports on locust campaigns. These data show only the districts and villages affected in a certain year during the mass outbreaks, but the most valuable data on the areas where the locust breeds during the minimum periods are not to be found in the reports. I have been able to make personally some observations on the subject in 1926 and 1927 in the Sierra de Guadarrama mountains, near

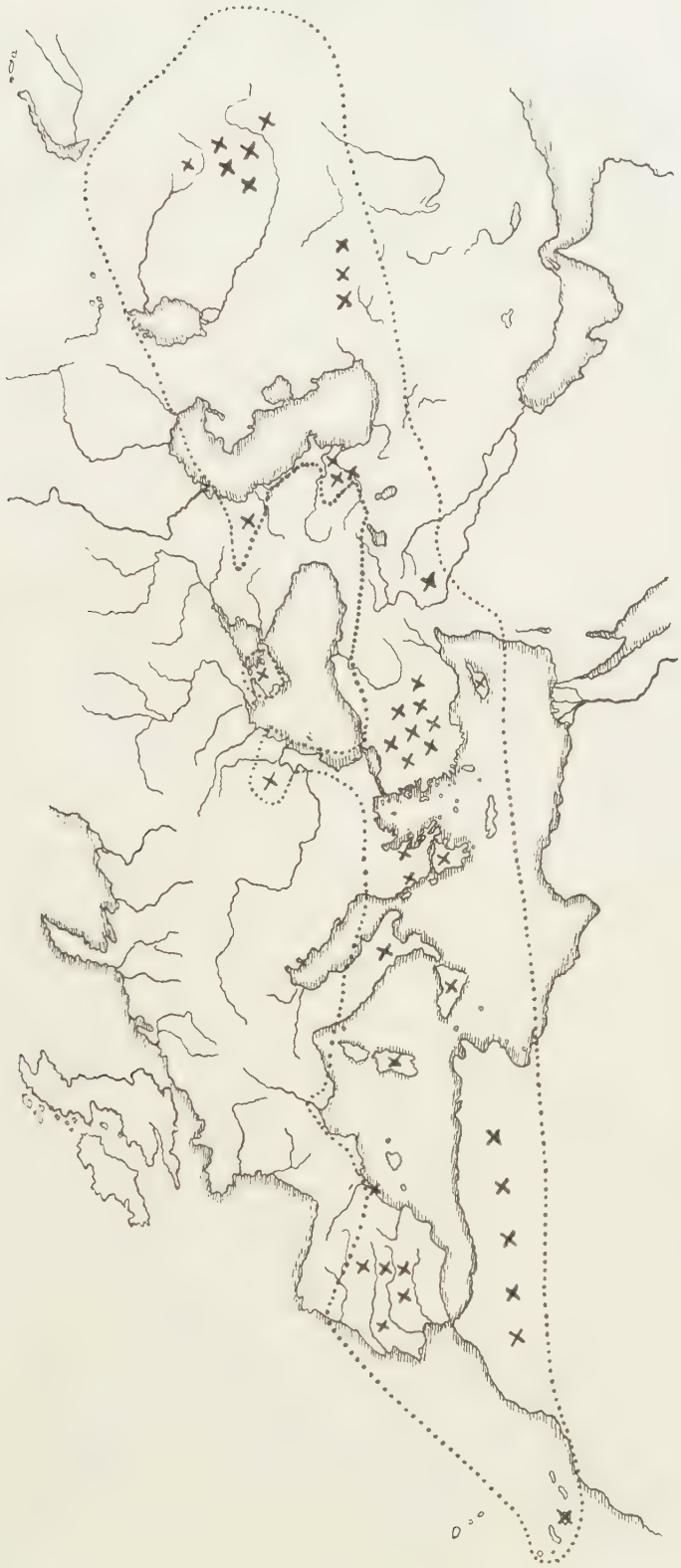

FIG. 83.—Area of distribution of the Moroccan Locust; the permanent breeding areas indicated by crosses (original).

Madrid. Isolated individuals of the locust occurred there at an altitude of about 5000–6000 feet on very dry stony slopes with sparse vegetation of *Juniperus* and other xerophilous shrubs and a few grasses ; the insects were to be found mainly on more open and even bare spaces with scattered grass. It is difficult for me to say whether these conditions may be considered typical for permanent breeding grounds of the Moroccan Locust in Spain ; judging, however, from some data communicated by Lapazaran (1925), breeding areas of this locust in the Aragon province must be similar to those observed by me. In the years of outbreaks, swarms of the locust descend on to the plateau of Central Spain, which represents a dry, grassy steppe, with mainly stony ground, occupied by crops. The enormous areas of uncultivated mountainous land, typical of Spain, present, apparently, ideal conditions for permanent breeding of this locust, but I believe that within these areas one could define the actual breeding grounds more precisely by studying exact ecological requirements of the species during the minimum periods.

In France this species appears as a pest only in the extreme south and then very seldom. The last outbreak occurred in 1918–1920, when swarms of the locust appeared in the semi-desert region of the lower Rhone Valley. No attempts to study the origin of the swarms have been made, and on the whole the distribution of the Moroccan Locust in its solitary form in the South of France is very insufficiently known ; it may be, however, stated that it occurs only in the coastal area of the Mediterranean. Grassé (1924) recorded the species from the sand dunes near Montpellier ; these ecological conditions are very exceptional for this species.

In Italy the Moroccan Locust is not often known as a pest, and the dates of its appearance and its distribution are not easy to establish, since the official reports speak of " cavalette," without more definite specific indication, and this name may also apply to *Calliptamus italicus*. So far as is known, the areas of distribution of the Moroccan Locust in Italy are to be found in the southern parts of the country, where there is some uncultivated, stony land. There are very favourable breeding conditions for the locust in Sardinia and Sicily, where it swarms fairly often ; breeding areas in Sicily, according to De Stefani Perez (1913), are on the dry, stony slopes of mountains.

In the Balkan peninsula this locust occurs mainly in the south, though it sometimes appears and even does damage in Montenegro (Baranov, 1924), but the data on its distribution there are inadequate, while nothing at all is known on its ecology. The same applies to Macedonia and Greece, where this locust undoubtedly occurs as a pest, though there is no reliable information about it known to me.

A classical country for the Moroccan Locust is Cyprus, where it did serious damage to agriculture up to the end of the last century, but has been reduced by well-organised control measures to the status of a solitary grasshopper and, what is more remarkable, has been kept in that state continuously since then by systematic destruction of incipient swarms (see below). The breeding areas in Cyprus are, apparently, all concentrated in the mountains of the central parts of the island.

The distribution and ecology of *Dociostaurus* in Asia Minor is relatively well known owing to the recent investigations of German entomologists (Bücher, 1918). The area of permanent breeding are the plateaus of Central Anatolia, and the western limits of the area are defined by the margin of the plateau ; the eastern boundary is not clear, but in the extreme East of Anatolia there appears to be a break in the distribution of the locust, and it reappears again much further south-east in the dry, stony semi-deserts on both sides of the middle course of the Euphrates, *i.e.* in Syria, Transjordania, and N. Iraq. As regards its ecology, La Baume (1918) describes the normal area for oviposition (Plate VI. 1) as slopes of mountains and hills, formed mainly of tertiary deposits and covered with hard loamy soil with stones, or else of limestone, also covered with loamy soil, including numerous fragments of stone. The vegetation in these places is very scanty and consists of small shrubs and some taller perennial plants with reduced leaves, mostly spiny and often strongly smelling. A considerable proportion of this vegetation is formed by *Astragalus* spp., *Anthyllis*, *Thymus*, *Erica*, *Cistus*, *Helianthemum*, which is very typical of such places, *Poterium spinosum*, etc. It may be stated fairly definitely that this type of vegetation arose in place of the exterminated forests or scrub (macchia), and that the wide distribution of the Moroccan Locust in Anatolia is to a large extent due to the destruction of natural forests. Oviposition in valleys and plains occurs only occasionally, though the larval bands and flying swarms usually move towards valleys ; the swarms, however, return for oviposition to the mountains.

The Euphrates area of the Moroccan Locust is practically unknown, and it even remains uncertain whether it is directly connected with the breeding areas in Northern Persia and Eastern Transcaucasia. Judging from the general conditions of the intervening regions of Turkish Armenia, there is every reason to think that the lack of reports on locusts from there is due simply to the backwardness of the country, but sooner or later the locust problem there is bound to arise.

The Transcaucasian breeding area is relatively well known. The breeding grounds there are concentrated in the dry foothills of Karabagh and, particularly, in the hills of the Persian Karadagh ; from here swarms of the locust often invade the fertile irrigated plains of Mugan, an important cotton-producing area, and inflict heavy damage ; they sometimes oviposit there, and two or even three generations may be produced, though permanent breeding is impossible.

Entirely unconnected with the preceding regions is a breeding area of the Moroccan Locust in the eastern part of the Northern Caucasus. Mass outbreaks of the locust there are known on the plains of the Atchikulak district, which have a purely steppe character of vegetation, and it appears that the actual permanent breeding grounds must be looked for in the foothills of the Daghestan mountains.

Another independent area lies in the Crimea, where this locust, however, appears very seldom ; the origin of locusts there is easily explained on geological grounds, since the Crimean peninsula represents a fragment of the Anatolian continent.

While the Transcaucasian area is intimately connected with breeding areas in Persia, these are still very little known, and the distribution of the Moroccan Locust in Persia in the southern and eastern direction is obscure. Unquestionable breeding areas are known in the Khorasan province of Eastern Persia, in the immediate vicinity of Russian Transcapsia. Indeed, it appears that there is a continuous chain of breeding areas along the dry Kopet-Dagh mountains that form the boundary between Persia and Russia. This chain probably continues still further eastwards into Afghanistan and through Bokhara into Russian Turkestan.

The last-named country is, undoubtedly, most of all entitled to have this locust named after it, since nowhere else does *Dociostaurus* play such an important part in relation to agriculture. The exact distribution of the locust in Turkestan and, especially, its permanent breeding grounds there are still imperfectly known. The reason for this is that, as elsewhere, all reports of breeding places are based on the observations made during mass outbreaks, when the emigrated swarms lay their eggs almost anywhere, provided that the mechanical properties of the soil are suitable ; on the other hand, no one is interested in the locust during the years of minimum, when the insects are to be found only in their permanent breeding areas and do no damage to crops. Still, the data collected by Siazov (1912) and Plotnikov (1926) permit us to conclude that the breeding areas of the Moroccan Locust in Turkestan are much more restricted than was formerly supposed. They are to be found fairly high up in the mountains, whence the swarms descend on to the cultivated plains only during mass outbreaks, and the locust can produce there two or three consecutive generations before disappearing. It is not definitely known how far eastwards the area of distribution of the Moroccan Locust extends in Turkestan, but it does not seem to occur at all in the Semiretchye province. Northwards from Turkestan the Moroccan Locust has been recorded as a pest from the Kirghiz steppes, but there is no doubt that these records are based on confusion with other species of *Dociostaurus*, which may appear as injurious solitary grasshoppers.

An extremely interesting area of habitation of the Moroccan Locust is presented by Hungary. The appearance of the locust there is stated to have occurred in 1888 (Jablonowsky, 1926), and since then, it has been necessary to practise control measures almost continuously. Jablonowsky states categorically that the locust did not exist in the country before 1888, but this is, of course, difficult to prove. According to that author, the appearance of the Moroccan Locust coincided with the disappearance of the Migratory Locust, due to the draining of extensive swamps in the Hungarian plains ; thus, instead of reed beds, where *Locusta* used to breed, dry steppes appeared, and these were populated by the Moroccan Locust. The latter lives there, apparently, under ecological conditions essentially different from those in other countries, but exact information on this important point is lacking. In any case, the example of Hungary shows that the Moroccan Locust may be able to extend the area of its permanent distribution if the opportunity arises.

With this we may conclude our somewhat lengthy survey of the distribu-

tion of this locust, and I will only add that indications in the literature of the occurrence of this species in Germany are obviously erroneous, while those from Rumania require confirmation.

To summarise the above information, we may say that the Moroccan Locust is intimately connected in its distribution with moderately high mountains, plateaus, and hills in the Mediterranean countries where permanent breeding areas are scattered. From these permanent areas, the locust can invade the plains from time to time and survive there for several generations, though not permanently. Since exact data on the location of the permanent breeding areas would be of the greatest importance in the control of this locust, work in this direction is not only highly desirable but necessary.

Bionomics

The conditions of oviposition have been described above in connection with the ecology of breeding areas, and it only remains to add that even the locusts that have migrated invariably lay their eggs in hard uncultivated soils. Another characteristic habit of this species is to oviposit in dense groups so that the egg deposits consist of more or less separate but very dense masses of egg-pods. How closely to each other the pods may be laid is shown by some figures given by Siazov (1912), who saw lumps of soil from deposits consisting almost entirely of pods, the density of the deposit being determined as 6000 pods to a square yard.

The number of pods laid by one female is not known exactly. Many authors refer to repeated ovipositions, but La Baume (1918) insists that these records are incorrect and due to observations not on a single female but on a whole swarm, the females in which may mature at different times. Observations in captivity are not convincing, since the development of the sexual products under artificial conditions may differ from the normal.

Oviposition begins at different times according to the geographical position of the area and its altitude, but, compared with other Acrididæ, the Moroccan Locust oviposits very early. Thus, in the plains of Anatolia, the eggs have already been laid at the end of May or early in June. The eggs, which only hatch in the next spring, have therefore a very long diapause ; at the end of summer the embryos in the eggs still have their heads pointing towards the posterior end of the egg. Plotnikov (1911), however, succeeded in hatching some larvæ in autumn, the eggs having been kept at a temperature 20–40° C. and under very humid conditions ; a mere raising of the temperature, without moisture, had no effect. This observation induced him to suggest that in nature hatching in autumn is not impossible, provided that the weather is abnormally warm and rain occurs. Normally this never happens in Turkestan, where the rains begin only when the weather becomes cooler. In any case there is no reason to doubt all official reports of autumn hatching of larvæ, though in most cases they are based on confusion with some other Acridids. At the same time, this may be one of the causes restricting the distribution of the Moroccan Locust to the dry mountains of the Mediterranean countries ; in a warmer and moister climate hatching of larvæ would often occur in

autumn, with the result that the winter cold would have to be endured by the hoppers which are less resistant than the eggs in their hard pods. According to Plotnikov, even a simple acceleration of development causing the embryo to hibernate at a later stage of development may be fatal to it.

Hatching occurs normally very early in spring, in March or April. Usually all larvæ from one deposit hatch more or less simultaneously, and hatching is over within a week or ten days.

The behaviour of the hoppers is typical of swarming locusts, and I will not describe it here, referring the reader to Chapter IV of this book. I might remark only that very typical of the hoppers of the Moroccan Locust is the formation of bands with an exceedingly long front—up to several kilometres —while the depth of the band is relatively very small.

The food of the hoppers consists of various plants. Sviridenko (1924) points out their special connection with the grass, *Poa bulbosa*, and other authors also agree that Graminaceous plants are their principal food, but nearly all other annual plants are also eaten. Shrubs, on the contrary, are avoided, and their leaves remain undamaged even after a band of hoppers has passed a night on them. Amongst such unacceptable plants are oleander, *Glycyrrhiza glabra*, *Vitex agnuscastus*, *Crataegus*, *Cistus*, *Poterium spinosum*, and some other shrubs common in the parts of Anatolia where the locust breeds permanently (La Baume, 1918); in Transcaucasia Sviridenko (1924) records as absolutely inedible the following plants: *Allium rubellum*, *Herniaria hirsuta*, *Adonis flammeus*, *Malcolmia contortuplicata*, *Euphorbia falcata*, *Malva transcaucasica*, *Plantago coronopus*, and *Artemisia*. It is very interesting to note that Sviridenko recorded wild poppies (*Papaver arenarium*) as eaten by the hoppers, while La Baume asserted that the cultivated poppy is never damaged by this locust.

Amongst cultivated plants grain crops mainly suffer from the Moroccan Locust, and these are still green at the time of the formation of the larval bands. Enormous damage is done by this locust in Central Asia and Transcaucasia to cotton plantations. On the other hand, very little is heard about damage to leguminous plants, particularly to lucerne, which is very extensively cultivated in nearly all regions where the locust occurs.

The larval development occupies five to six weeks, and the final moult in a given swarm occurs within a short time.

After acquiring wings, the locusts make some circular flights, and, if the swarms are very large, a direct emigration flight may follow, but it is never so prolonged as in other locusts.

Nothing is known of the development and behaviour of the species in its solitary phase in the permanent breeding grounds.

Periodicity

No regular periodicity in the outbreaks of the Moroccan Locust in any one country can be noticed, but the number of locusts is subject to very strong and sudden irregular fluctuations. Particularly remarkable is an extremely rapid rate of increase when swarms appear in temporary breeding areas; this

leads me to suggest that the ecological conditions of the permanent breeding grounds may be very favourable to the normal existence of the locust, but that the rate of its increase there is slow; once, however, some considerable swarms are formed, they emigrate to the temporary areas, where a sudden increase in the rate of multiplication is observed. The ecological conditions of the temporary areas seem to be unsuitable for permanent habitation of the locust, but are very favourable to sudden outbreaks.

The factors causing the periodicity of outbreaks are entirely unknown. Plotnikov (1911) believes that, since the embryonic diapause is caused by dryness, an abnormally warm and damp autumn may result in the premature hatching of hoppers and their mass destruction. On the contrary, abnormally dry weather would increase the chances of embryos surviving the winter, and an increase in the numbers of locusts may result. This theory seems sound, but much experimental work on the influence of external conditions on the development should be done before it can be acccepted; so far, not even a beginning with such experimental investigations has been made.

There are no sharply defined solitary and swarming phases in the Moroccan Locust, though when specimens from Cyprus, or from Spain, in both cases taken as solitary grasshoppers, are compared with specimens from swarms, it appears that the latter are, on the average, larger, less brightly coloured, and their elytra are relatively longer (Fig. 81). Baranov (1925) has even described from Montenegro a "dwarf race" of the Moroccan Locust. Colour differences of this form, which occurs, not in the swarms, but near them, consist in its being paler and brighter, while the colours do not become brown towards the end of the individual life, as they do in the swarming form. The morphological characters of this form are its smaller size, acute vertex, acute posterior angle of the pronotum, sharp frontal ridge (it is not quite clear what the author meant by this name); there are also some differences in the male genitalia. The measurements of the two forms are as follows:

	Normal males.	"Dwarf" males.
Ratio of the height of head to diameter of an eye	3·33	2·75
Ratio of width of head at the base to its length above ..	1·36	1·16
Ratio of length of antenna to length of pronotum	1·44	2·00
Ratio of length of elytra to length of hind femur	1·85	1·45
Ratio of length of hind femur to length of pronotum	2·14	3·20
Ratio of length of hind femur to length of middle femur ..	2·55	3·48
Ratio of length of middle femur to length of pronotum ..	1·02	0·94
Ratio of length of elytra to length of pronotum	4·80	4·85

Baranov considers particularly important the ratios of the head measurements and the relative length of the hind femora, while the variation in the length of the pronotum, middle femora, and elytra is correlated with that in the general size of the insect. He characterises the form, which he considers to be at least transitory to the solitary one, by the following main characters: head long, eyes large, antennæ long, hind femora long—of course, all comparatively with the swarming form. He suggests for this form the name *degeneratus*, and considers it a "race."

Whether *degeneratus* may be really considered the solitary phase of the Moroccan Locust is difficult to say at present. Further work on this problem

is very urgently needed, since its solution may help considerably in the study of the problem of periodic outbreaks. Particular attention should be paid to observations on the Moroccan Locust in its permanent breeding areas in the years of minimum, and a study of larval characters and of behaviour would be of special value.

Natural Enemies

I will not give here a full list of the known natural enemies of the Moroccan Locust since it may be easily compiled from the lists given in Chapter VI, but I would like to draw attention to the fact that practically all the data in those lists are based on observations during the years of mass outbreaks, that is, not in the permanent breeding areas. In other words, we know at present only some of the parasites that may play a part in the reduction or suppression of an invasion, but nothing is known as to those enemies of the locust that regulate its numbers in the permanent breeding areas, though they are of particular interest.

It may be remarked that the Moroccan Locust seems to be entirely immune from the fungous disease caused by *Empusa grylli*, though the lack of records may be due to the fact that this locust inhabits countries with a very dry climate that is unfavourable to the fungus.

The Locust Problem in Spain, Transcaucasia, and Turkestan

Though the Moroccan Locust, as we know, inhabits a very large area, it is only in certain parts of it that its presence is a source of an almost continuous and very grave locust problem; in others this locust is merely a more or less occasional pest.

The most important locust of Northern Africa is not this species, but *Schistocerca gregaria*, and it would be more convenient to discuss the locust problem in that country in connection with this latter species (see Chapter XII). As regards the Moroccan Locust, its outbreaks in Morocco, Algeria, and Tunisia are relatively not very frequent and are only of moderate importance, since invasions of the cultivated areas by swarms bred in the mountains are the exception rather than the rule. Nevertheless, particularly in Algeria, this species sometimes plays an important part, and the most recent example of its activity is in progress there at the present time. There is little doubt that, with the extension of agriculture in North Africa, when areas under crops become larger and are situated nearer to the breeding grounds of the locust, the situation will change in a direction decidedly unfavourable to agriculture.

Very similar conditions exist in Anatolia, where, however, the Moroccan Locust has more than once been the direct cause of widespread destruction of crops and general famine. The misery of the population during these periods of locust invasions is still further aggravated in that country by the archaic methods of control, which necessitate the use of forced labour, the recruiting of which is regarded by the subordinate administrative officers as a source of revenue for their own pockets. The anti-locust campaigns organised in Anatolia by German entomologists during the Great War (Bücher,

1918) demonstrated most convincingly that the control of locusts in that country on a large scale is a practical possibility, but the effectiveness of the organisation depends entirely on the soundness of the general administrative system. The importance of locusts in Anatolia will inevitably increase with the growth of agriculture in the country, and the locust problem there is bound to become one day of supreme importance.

In Italy, particularly in Sicily and Sardinia, the Moroccan Locust sometimes causes serious damage, but nothing like a regular locust problem is created by it. *Calliptamus italicus* is the more usual pest there, and it would be better to discuss the general problem of locust control in Italy when dealing with that species (see Chapter XV).

A fairly serious part in the local economic position is played by this locust in Hungary, where it has appeared relatively recently as a pest (see p. 228). Its persistence there may be attributed, first of all, to the insufficiently effective methods of control in general use (crushing with horse-drawn iron brushes, see p. 172) and to reliance on the execution of the work by landowners and rural communities ; the abolition of this system and the adoption of a central state organisation, provided with funds sufficient to conduct campaigns with poison baits and paid labour, would speedily lead to the complete solution of the locust problem in Hungary. Another important point to which attention must be paid is the study of the ecological conditions under which the Moroccan Locust breeds in that country, since it seems not impossible that this has some connection with overgrazed pastures which bring about artificial conditions that favour the breeding of the locust. Some very valuable work on ecological lines has already been done in Hungary (Jablonowsky, 1926), and it would be necessary only to carry it further and to study the problem in more detail.

Amongst other countries where the Moroccan Locust occurs, France can be left out of consideration, since the outbreaks there are very rare. In Northern Syria and Mesopotamia the low level of agriculture makes the locust problem of little importance at present, but it will claim attention in time. In the Balkans, outbreaks only occur occasionally, and no serious locust problem exists. In the last century Cyprus passed through a very trying period of locust activities, but at present the pest is kept under control by an efficient system of continuous supervision of breeding grounds and suppression of incipient swarms.

In contrast to all the countries just discussed, the Moroccan Locust constitutes an almost permanent and very serious economic problem in Spain and Portugal on the one hand, and in Transcaucasia and Turkestan on the other. The present position with regard to its control in these countries and the means for improving the position merit special discussion.

In the Iberian peninsula the Moroccan Locust, as we know, finds eminently suitable conditions for permanent breeding, but its presence is realised only when it is well on the increase and cultivated valleys are invaded. This occurs in different provinces almost continuously, and the locust problem in Spain and Portugal is practically permanent, though very extensive measures are carried out for the control of locusts and large numbers of them are exterminated.

Although the causes of the relative ineffectiveness of control measures in Spain are partly realised by those who are directly connected with locust control, they escape their attention to some extent owing to a certain conservatism and also to the desire to avoid too drastic alterations in the present system. The latter is based, on the technical side, on the use of a number of varied methods, very great importance being attached to the autumn and winter campaign for destruction of eggs in the ground. This is done by ploughing and harrowing the lands where egg deposits are reported. To ensure the possibility of these operations, a preliminary survey of deposits is presumably carried out, but all the official reports are strangely silent as to how the survey is actually made. Apparently the information is collected officially, landowners and rural administrations being obliged by law to report egg deposits. Since a report is bound to result in an order to carry out the very costly operations of ploughing or digging often on some hardly accessible mountain slopes, it is easy to imagine that no reports are forthcoming if the fact of the infestation can be safely concealed. Legal penalties would be levied on the offenders, but this does not contribute to the success of the particular campaign.

Further, the effectiveness of any operation tending to destroy eggs in the soil is very doubtful (see p. 171). Even if a certain proportion of eggs is actually destroyed, this does not amount to the annihilation of all eggs, and the necessity for control measures against the hoppers in spring still remains. Since the cost of work by poison baits depends not so much on the density of locust bands as on the area occupied, there will not even be a reduction in the cost of the spring campaign on the lands where eggs were " destroyed " or collected. The moral effect on the population of the appearance even of small bands of locusts on lands, where weeks of heavy work have been spent, must also be borne in mind.

It seems therefore abundantly clear that the practice of attempting to destroy or collect egg-pods should be entirely abandoned, and the system of control should be based wholly on the measures to be taken against the hoppers in spring.

Here again very much depends on an exact knowledge of the places where hatching may be expected, and this information cannot possibly be expected to be exhaustive, when it is supplied by landowners, who will be obliged to take measures to control the locust ; obviously such information will be withheld in every case where there is a chance of its not being discovered.

Technical means in use for the control of the locust in Spain are not standardised, and any method can be, and is, used which gives some results. Trenches, barriers, trampling, burning, external insecticides, etc., are used independently and in combination. Now this confusion of methods leads to a complete absence of results, the more so as the methods most favoured are those that are inferior in efficiency. Thus external insecticides are used on a very large scale, but they are both exceedingly expensive and only partly effective ; on the other hand, poison baits are not in use, though their possibilities and advantages are known to local entomologists (Lapazaran, 1925). Neither

are barriers used as extensively as they should be in a mountainous country where they can be most effective.

From the technical point of view, the solution of the locust problem in Spain and Portugal clearly lies in the universal adoption of poison baits and barriers, while the autumn and winter campaigns directed against the egg masses should be abandoned as useless and too costly.

The improvement in the technique alone, however, is not sufficient, since the system of organisation leaves much to be desired. To begin with, the handling of the campaigns is not centralised, but every Province has to organise its own (the State only giving some financial assistance when required), and worse than this, every rural community carries it on more or less independently. There is no entomological organisation either at the head of affairs or locally, and the work in the Provinces is in charge of agricultural officers (*ingenieros agronomos*), who in locust years have to abandon all their normal duties and act as entomologists, though they have no special training as such. The actual working parties consist of workmen who are either " voluntary " (*i.e.* forced by law to work), or only partly paid ; there is no need to repeat here the obvious disadvantages of this system (see p. 206).

Thus the causes of the permanency of the locust problem in Spain and Portugal are numerous, but not difficult to remove. A competent central organisation would very soon elaborate variations of technical methods (baits and barriers) suitable for local conditions and reform the system of their application, so that the really essential starting-point towards the solution of the problem would be the establishment of a central entomological organisation for the control of pests (as opposed to an organisation for their study). The abolition of the autumn and winter campaigns would release very considerable funds, which would make it possible to conduct the spring campaign on the basis of fully paid labour.

The question of international co-operation between Spain and Portugal must be also settled in some effective way ; otherwise the border regions of the two countries will be always blaming each other for invasions of locusts.

Parallel with the reorganisation of the direct control of locusts, there must begin measures that aim at the prevention of outbreaks. The first step would be a study of all the existing breeding grounds from the point of view of their location and their ecological conditions. However widespread the locusts are in Spain, there is no doubt that they are not omnipresent even in years of outbreaks, when an extension of their area takes place ; in the years of minimum, the locusts must retreat to a limited number of breeding grounds, which can be located and studied in detail. The first step in this direction can be achieved by studying the history of previous invasions and finding out their origin, though the actual work can of course only be done on the spot and by fully competent entomologists with an understanding of ecology. If breeding grounds could be located in this way, a service of continuous observations on the development of locusts can be instituted in order to suppress incipient outbreaks. At the same time a detailed study of the ecological conditions of the breeding grounds may lead to practical means of suppressing them for ever.

Another area where the Moroccan Locust is almost a permanent problem is the Caucasus and Turkestan. In the latter country particularly, depredations caused by this species have always been, and still are, of enormous dimensions, and its economic importance is especially great because these are the only regions of Russia where cotton growing on a commercial scale is possible, and these cotton plantations are under a constant menace from locusts. The situation was exceedingly grave up to very recent times, in fact, so long as control measures were based on the time-honoured methods of ditches, etc., and the organisation relied on forced labour. An excellent summary of locust control in Turkestan by Siazov (1912) abounds with enormous figures of the damage caused by locusts, and at the same time reveals the stupidity of using forced labour for the control of locusts in a country where the bulk of the population is not even agricultural. The ineffectiveness of control methods that annually swallowed up enormous funds led to drastic reforms in the organisation; this passed into the hands of entomologists, efficient chemical methods were introduced, and at the period of the Great War, the locust problem in Turkestan and in the Caucasus might have been considered solved. Difficulties of obtaining chemicals, shortage of labour and funds, etc., during the War made it very difficult to conduct campaigns on a large scale, and finally the years of revolution and of civil war in the country, when organised campaigns were impossible, have resulted in the locust again gaining ascendancy. At present, however, the situation is once more well in hand, thanks to the entomological organisations, and the control campaigns are conducted in a most efficient way, and on a scale which would seem fantastic in some other countries. It is not a patriotic pride in my own country that compels me to state that the control of locusts in Russia, both from the point of view of organisation as well as of technique, is far ahead of any other country in the world. It is the result of an unprejudiced comparative study of the locust problem in all countries. The technique in use is poison baits, though at first the practical possibility of controlling locusts on a large scale by arsenical spraying was demonstrated by Russian entomologists. The organisation is based on centralisation in the hands of State entomological institutions and on fully, or at least partly, paid labour.

Though the immediate results of the Russian campaigns are very satisfactory, the locust problem in Turkestan and the Caucasus does not cease to be a problem that requires continuous attention and expense. This is due to the fact that entomologists are always handicapped in their work by the slowness of official machinery, resulting in the funds for the organisation of campaigns being nearly always provided too late. It is also difficult to obtain funds at all when the locusts are still in small numbers, and they are more readily given when the outbreak is at its maximum and when it is more difficult to check. Further, there has been made so far no attempt towards a definite policy of controlling locusts in their breeding grounds and in respect of the breeding grounds themselves. Entomologists in Russia are, however, awakening to the necessity of concentrating on these, and there is no doubt that we shall not have to wait long for practical steps in that direction.

CHAPTER XI

THE MIGRATORY LOCUST (Locusta migratoria, L.) AND THE LOCUST PROBLEM IN RUSSIA AND THE TROPICS OF THE OLD WORLD

Description of Stages

Adult of the Northern Swarming Phase (ph. *migratoria*, L.) (Figs. 67, 84).—Antennæ slender, moderately long. Face in profile vertical; frontal ridge convex; vertex sloping forward. General coloration greyish-green, or yellowish (sexually mature males become bright yellow, while females at that period become brown). Mandibles black-blue. Pronotum with a distinct constriction in the middle; often with two dark stripes along the upper surface; median keel low, in profile straight; front margin of the pronotum straight, hind angle rounded. Elytra with dense, small brownish spots. Wings hyaline, slightly greenish, or yellowish. Hind femur shorter than half the length of the elytron. Hind tibiæ usually greenish, seldom reddish. Length, male 40–50 mm., female 42–55 mm.; elytra, male 42–54 mm., female 46–56 mm.

Adult of the Tropical Swarming Phase (ph. *migratorioides*, Rch. & Frm.) (Fig. 70).—Similar to the preceding in colour and general appearance, but the pronotum very strongly constricted in the middle; median keel very low, in profile concave; hind margin of pronotum rounded.

Adult of the Solitary Phase (ph. *danica*, L.) (Fig. 67).—Coloration variable, often green, sometimes blackish. Pronotum strongly compressed laterally, but practically without a constriction in the middle; median keel high, roof-shaped, in profile convex; front margin of pronotum angulate; hind angle acute. Hind femora longer than half of the elytron. Hind tibiæ almost always red. In other characters similar to the swarming phases. Length, male 29–35 mm., female 37–60 mm.; elytra, male 33–43 mm., female 40–58 mm.

The determination of the phases is not always possible, since the extreme forms are connected by transitional ones.

Hoppers of the Swarming Phase, First Stage.—Antennæ 13–14-jointed. Black, not shining, with a yellowish-white median stripe along the back and a narrow yellowish line behind each eye; margins of pronotum with a narrow wavy yellowish fringe. Hind lower angles of mesonotum and metanotum rounded. Hind femora with three indistinct pale fasciæ. Length at the beginning of the stage 7–8 mm.; at the end 9–10 mm.

Hoppers of the Swarming Phase, Second Stage.—Antennæ 18-jointed. General coloration black, with some brownish-yellow markings. Head brown,

with two velvety-black spots on the vertex. Pronotum with two large velvety-black spots on the sides. A yellowish median stripe runs along the median keel of the pronotum and extends also on to the abdomen where it is included between two velvety black stripes. Rudiments of elytra and wings distinct, angulate. Hind femora yellowish-grey or dirty-brown, without fasciæ. Length 10–14 mm.

Hopper of the Swarming Phase, Third Stage.—Antennæ 20–21-jointed. In the coloration brown predominates. Pronotum in the middle velvety-black, on the front margin edged with whitish, sometimes bluish, streaks; sides yellowish-brown. Rudiments of elytra and wings very distinct, black,

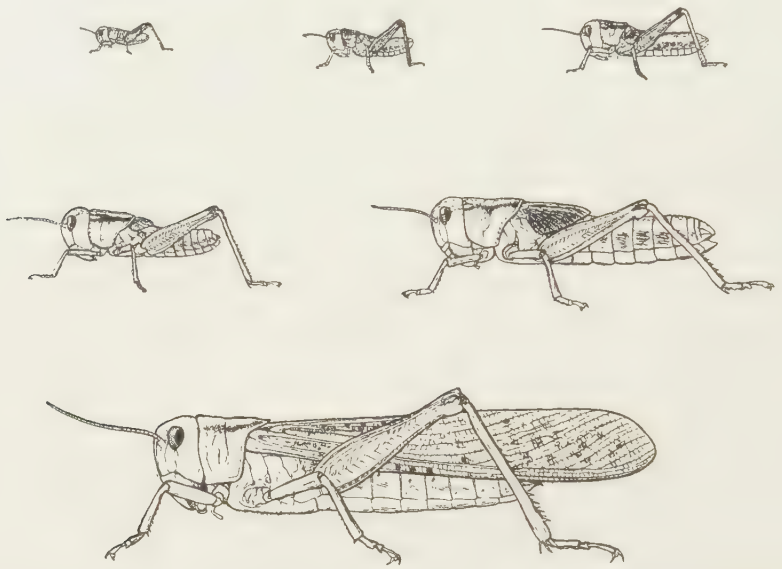

FIG. 84.—Migratory Locust, stages of development; natural size (after Plotnikov).

directed obliquely backwards and downwards. The pale median stripe of the abdomen included between two velvety-black ones, below which there runs a yellowish-grey stripe. Length 15–21 mm.

Hopper of the Swarming Phase, Fourth Stage.—Antennæ 22–23-jointed. General coloration paler than the third stage. Head wholly pale-brown, with two small black spots on the vertex; yellow postocular stripes become very sharp and edged with brown. Pronotum above velvety-black with the keel pale, hind margin narrowly yellow, sides brownish-yellow. Rudiments of elytra and wings, turned upwards on to the back, black. Abdomen as in the third stage, but paler. Length 24–26 mm.

Hopper of the Swarming Phase, Fifth Stage.—Antennæ 24–25-jointed. General coloration brown, with reddish tinge. Head brown, somewhat reddish. Pronotum as before. Rudiments of elytra and wings large, black, with a narrow yellowish margin. Length, male 25–36 mm., female 32–40 mm.

Hoppers of the Solitary Phase.—No descriptions of hoppers of early stages exist. In the later stages the hoppers are of varying colour, usually

green, or of the colour of dry grass, sometimes grey or coal-black, but always without any definite pattern, without velvety-black stripes and without any reddish-brown or yellow colour. As in the adults, transitional forms between the solitary and the swarming phases may be observed, so that it is not always possible to determine the phase exactly.

Fig. 85.—Egg-pods of the Migratory Locust; natural size (redrawn after Nikolsky).

Egg-pod (Fig. 85).—Shape very variable, more often bow-like, or bent at an angle, sometimes almost straight. Outer envelope very thin, brown, consisting of the hardened secretion of glands; of the same substance consists the upper part of the pod, or its stopper, occupying from one-fifth to one-fourth of the pod. Eggs in the pod are arranged in four rows and glued together by the same gland secretion; their number varies from 55–115. Length of the pod with the stopper 58–75 mm. Egg about 7 mm. long; its chorion with spinules connected by ridges (Fig. 24, L).

Distribution and Ecology

In discussing the distribution of the Migratory Locust, it is more convenient to begin with the solitary phase (ph. *danica*). Its distribution, though limited to the Old World, is extremely wide; indeed, no other species of Acrididæ with such a wide area of distribution is known (Fig. 86). It is therefore simpler to state where *danica* does not occur, *viz.* the colder regions beyond the 60th parallel N. and S., in the dense tropical forests, and in waterless deserts; in mountainous regions *danica* ascends to great altitudes, occurring in the Himalayas up to 15,000 feet.

As regards ecological conditions, the solitary phase is not very particular, occurring under widely varying conditions so that it would be difficult in the present state of our knowledge to define its ecological requirements.

Within the enormous area of distribution of the solitary phase, there are certain regions where the formation of the swarming phase is possible and happens periodically. The tropical swarming phase, ph. *migratorioides*, has as yet been very little studied with regard to its distribution and ecology.

In Africa *migratorioides* sometimes appears in the Cameroons and in Togo, apparently in connection with somewhat swampy places. There also appear to be some breeding areas of this form in East Africa, since swarms of it have been recorded in the Kilimandjaro district (La Baume, 1910).

In Madagascar *migratorioides* is very widespread and of great economic importance; its breeding areas there are connected with swamps overgrown with reeds, though actual oviposition occurs at some distance from the edge

of swamps (information received from Mr. B. Zolotarevsky, at present studying this locust in Madagascar).

In tropical Asia this locust has been studied in the Federated Malay States where an outbreak occurred in 1913–1914. Unfortunately the observations were made in the years when a migration of swarms was in progress so that

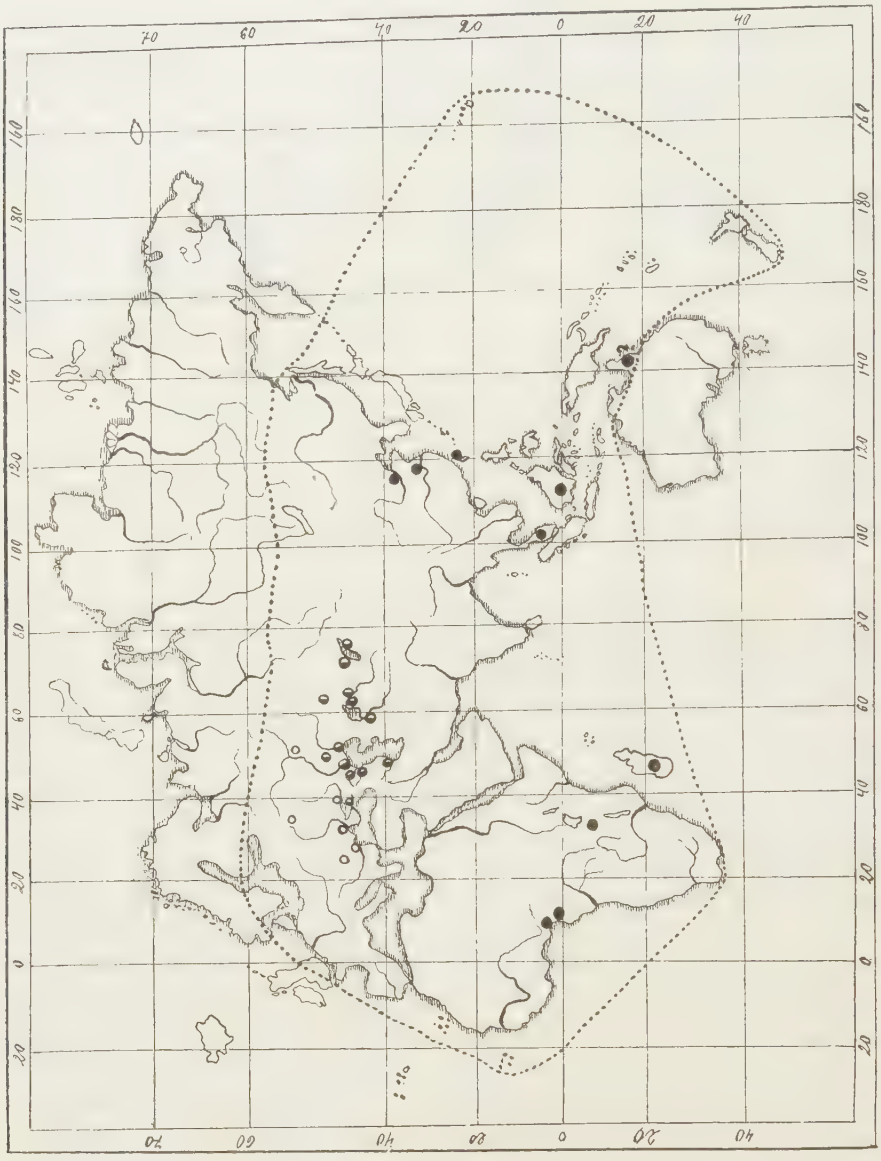

Fig. 86.—Area of distribution of Migratory Locust. A dotted line delimits the area of the solitary ph. *danica*; black circlets, breeding areas of ph. *migratorioides*; half-black circlets, ditto of ph. *migratoria*; white circlets, areas of occasional breeding and extinct breeding areas (original).

the ecological data obtained are not very reliable, since it is known that oviposition by swarms that have migrated often takes place in localities that are not typical for the species. The most favourite habitat of the locust there is the, so-called, lalang land, *i.e.* areas where natural forest has been destroyed and a jungle of lalang (*Imperata arundinacea*) has taken its place. Where the

growth of lalang is thick, covering the ground to a height of 3–4 feet, abundant food is present for hoppers and adult locusts, but this is not a suitable place for oviposition, on account of the soil being too much covered by grass. After a lalang fire, which may expose the soil over several square miles, ideal conditions for egg-laying exist until the lalang is again thick and tall. In very poor soil the lalang is always sparse, and conditions are always suitable for breeding. Another type of breeding place in Malayais presented by abandoned tin mines, where large areas are covered with sand and stones from the mines ; such a soil supports a sparse flora, chiefly of grasses, and the conditions are suitable for oviposition (Pratt, 1915). It will be noticed that both kinds of breeding places are due to human interference, and this indicates, on the one hand, that favourable conditions for the breeding of the locust may be directly produced by certain cultural methods ; on the other hand, some natural breeding places are certainly to be expected in this region ; these must be looked for in localities with a relatively sparse grass vegetation, probably at the edges of jungle.

It is not very definitely known which swarming phase of the Migratory Locust occurs in China and Formosa ; apparently in the latter country it is *migratorioides* (Takahashi, 1925), and in China *migratoria* (Chang, 1925). There are no data on the ecology of the locust in these two countries.

In the Philippine islands *migratorioides* is of enormous economic importance, but there is little definite information available on its distribution and ecology there beyond the fact that the breeding areas are connected with immense jungles of bamboo and reeds (Hernandez, 1921).

Breeding areas of *migratorioides* also exist on some of the islands of the Malayan archipelago, in North Borneo, for example (Uvarov, 1921), but nothing definite is known about them.

In the North of Australia, some swarming phase of the locust appears occasionally in Queensland in large numbers (Girault, 1913), but even the systematic data are in this case somewhat confused (see p. 303). In New Zealand the solitary phase occurs fairly commonly, but it differs there a little from typical *danica* owing to its smaller size, darker general coloration, and less sharply defined morphological characters characteristic of this phase ; in all respects it is analogous to the Central Russian form, which will be discussed later.

Let us now study the distribution of this locust in the temperate regions of the Northern hemisphere. The solitary phase, as stated above, is here also widely distributed, but the places where the swarming phase occurs are relatively very restricted. Thus, the swarming phase is remarkable for its absence from the whole of North Africa, the Lower Nile valley included. The centre of distribution of *migratoria* is undoubtedly in Central Asia, and its breeding grounds there can be even more precisely defined owing to recent research by Russian entomologists, particularly Nikolsky (1925). I will here give only a brief outline of the main breeding areas in Central Asia and South Russia.

Very extensive breeding grounds are to be found in the valleys of the middle and lower reaches of Syr-Darya and Amu-Darya amongst vast growths

of reeds (*Phragmites communis*, L.). Farther to the east, similar conditions exist in the basin of Lake Balkhash and of its tributaries (river Ili and others) on the shores of the Ala-kul lake, Zaisan and some lakes in Northern China.

In the basin of the Caspian sea *migratoria* has permanent breeding grounds in the lower reaches and deltas of practically all the rivers flowing into it. The more important are those on the Volga, Kuma, and Terek.

Several less important breeding grounds are known on the shores of the smaller lakes and rivers around the Caspian sea, but they may be left out of consideration. A full discussion of the Russian breeding grounds can be found in the Russian edition of this book and also in Nikolsky's monograph of the Migratory Locust, 1925.

Farther to the west, there are also some areas that until quite recently served as breeding places for the swarming phase, *e.g.* some reed jungles on the lower Kuban, where the locusts were common until 1884, since when they disappeared, only to reappear again in 1920 for a short period. Approximately the same period, the 'eighties of the last century, marked the disappearance of swarms of the locust from the lower reaches of other rivers emptying into the Black Sea—Don, Dnieper, Bug, Dniester and Danube, where the locust had hitherto bred periodically in large numbers.

In Western Europe no breeding areas of *migratoria* exist at present, though they apparently did so at some remote, prehistoric period. All the data of later invasions of locusts in Austria, Germany, etc., must be based on migratory swarms from the Danube breeding grounds and from temporary ones established by such swarms (Filipjev, 1926*a*). An exception occurs in Hungary, where permanent breeding places of *migratoria* existed until relatively quite recently in the plains on the middle Danube and its tributaries (Jablonowsky, 1926).

To the north of the zone of breeding grounds stretching along the shores of the Black, Caspian, and Aral seas, there is another zone, not very important from the practical point of view, but very interesting theoretically and lying within the steppe and steppe-forest regions. The distribution and ecology of the locust there has only become known quite recently thanks to the exceptionally interesting investigations of Predtechensky (1925).

After this brief survey of the geographical distribution of the areas where breeding of the swarming phase is possible, we will turn our attention to the ecological conditions.

As regards the tropical regions, breeding of the swarming phase (*migratorioides*) appears possible in more or less open places, with relatively dry soil, amongst jungles of bamboo, reeds, and tall grass. There also occurs a form which may be mistaken for *migratoria* of temperate latitudes, but which represents there a transitional form between typical *migratorioides* and *danica*. More exact data on the ecology of this locust under tropical conditions are lacking.

Much better known with regard to their ecology are the Russian breeding grounds. Central Asian areas have been especially studied by Nikolsky (1925), and he gives the following description of their ecological conditions. The

river beds in their lower reaches are very inconstant ; new channels are often formed, while old ones are filled with sand and transformed into shallow lakes, which gradually dry up. This drying up of lakes results in an ecological succession of vegetation ; the bottom of a dry lake is covered first with low-growing reeds (*Phragmites communis*), then hygrophilous plants like *Scirpus*, *Typha*, and *Juncus* appear ; later mesophilous grasses (*Agropyrum repens*, *Elymus aralensis*, *Atropis distans*, *Aeluropus littoralis*, etc.) develop, and these give way in their turn to xerophilous forms. It is the stage when mesophilous grasses, with some admixture of low-growing *Phragmites*, cover the bottom of a dry lake that Nikolsky considers most favoured for oviposition by the migratory phase. Thus, the actual breeding places of *Locusta* in Central Asia, although in the middle of enormous reed beds and amongst numerous channels and lakes, cannot be described as swamps, as is commonly done. Indeed, here, as in the tropics, the actual breeding places are connected with relatively very dry spots amongst a dense vegetation of reeds and tall grasses ; the vegetation offers an unlimited supply of food, but for oviposition the locust selects more open and drier spots. Analogous observations have been made elsewhere. Thus, my investigations (1911 ; see also Zacharov, 1927) in the Kuma valley (Northern Caucasus) have shown that the locust selects for oviposition almost exclusively what are locally called " islands," *i.e.* more elevated places amongst reed beds, while the latter are evidently avoided. The " islands " specially preferred for oviposition are those that are covered with moderately tall and not too dense grasses, like *Bromus inermis*, *Triticum repens*, and an admixture of isolated, short plants of *Phragmites*.

All these data prove that regions where the swarming phase can be produced are characterised by an extensive development of reeds, bamboos, and similar tall plants, but there must be also some more open spaces with shorter vegetation and drier soil for oviposition. It seems, therefore, that reeds and similar plants are necessary mainly as being the most suitable food, but there is some reason to think that the connection between the locust and reed beds may be to a certain extent due to the climatic regime of the latter, at least in temperate regions. The climatic conditions of reed beds in Central Asia, though they have never been closely studied, are very peculiar and differ widely from those of the surrounding deserts and steppes owing to their humidity and higher mean temperatures ; in other words, the climate is of a more or less tropical type. These peculiar conditions of reed beds make them very suitable for mass development of the locust, and the appearance of large numbers of hoppers in a particularly favourable year leads automatically to transformation into the swarming phase ; after that a further increase in numbers goes on at an accelerated rate (see p. 160).

These suggestions are, of course, largely theoretical and require detailed experimental work to check them, but I think it useful to advance them in order to attract attention to the necessity of thorough studies in the ecology of breeding grounds ; without such investigations we shall never be able to understand the causes of periodicity or to approach the problem of controlling the breeding grounds for prevention of locust outbreaks. Extremely important

in this respect would be studies of the breeding grounds that have ceased to function relatively recently, such as those in the deltas of the rivers flowing into the Black Sea. The disappearance of the breeding grounds there is usually ascribed to " the advance of agriculture," but what the exact cultural measures are that have rendered these localities unsuitable for the swarming phase (the solitary one still occurs there) remain obscure. The actual reduction in the area under reeds is insufficient to have caused a lack of food for the locusts ; cultivation has occupied only very few scattered spots, so neither can this be the direct cause of the disappearance of locusts. It would appear that even a very slight alteration in the ecological conditions is sufficient to prevent the formation of the swarming phase, but what these factors are is unknown ; some ecological work on this point is now being carried out in Russia, but the results have not yet been published.

The part played by the climatic conditions in the formation of the swarming phase is evidenced by the differences in the tropical swarming phase (*migratorioides*) and that of the temperate regions (*migratoria*). The first is undoubtedly more modified, as compared with the solitary form, than the second, and this may be due to climatic conditions. One might suggest that the present Central Asiatic breeding areas of *migratoria* were once able to produce *migratorioides ;* this might have been the case when the climatic conditions of Central Asia were subtropical if not tropical, as they probably were in one of the past geological epochs. Alterations in climate towards the present conditions were insufficiently great to make the formation of the swarming phase an impossibility, but the present climate is not sufficiently hot and damp to ensure the full transformation of *danica* into *migratorioides*, and it stops half way, so to speak, at the *migratoria* stage.

This view finds support in the observations on the Migratory Locust in still more temperate regions, particularly in the forest-steppe zone of Russia. The ecology of the locust there differs essentially from that described above ; in that region the locust inhabits fairly high open spaces amongst forests, with dry and warm soils (Predtechensky, 1925). The mass development of locusts only occurs there very exceptionally, and, what is most remarkable, the swarming phase proves to be much nearer to the solitary one than is the case with the southern form. In this case, it would seem that the climatic conditions are insufficient for the formation of even typical *migratoria*, and a swarming phase very near to *danica*, but still recognisably different from it, is the result. Still farther to the north, the formation of the swarming phase becomes impossible, though the solitary phase can exist.

The origin of these, practically extinct, breeding grounds so remote from the others may be explained also on a geological basis, since extensive deposits of peat in Central and even Northern Russia denote a very great development in the past of swamps containing reeds, similar to those existing in Turkestan at present. It is natural to suggest that the locust was then also more widely spread and that regular breeding grounds of *migratoria* existed farther north than is now the case. With the advent of a colder climate, they became extinct, but the locusts have survived in the solitary form and are able to produce

something approaching the swarming phase in years with abnormally high temperatures. A similar course of events may have occurred in Western Europe, where small colonies of the locust still exist in some places (on the Rhine, Bodensee, etc.), though no swarming phase is ever produced. It is specially worthy of remark that the solitary phase of Western Europe is very similar in its coloration and morphological characters to that of New Zealand, and this may be again explained on climatic grounds.

Bionomics

I do not propose to discuss the bionomics of this species in all its details, since numerous data on its development, behaviour, etc., are scattered over the general part of this book.

The annual cycle of development is different for the swarming and the solitary phase, being in the latter directly dependent on the actual climatic conditions, while in the former a definite annual cycle of development exists (see p. 153). In temperate climates the cycle corresponds to one generation in a year, but nothing definite is known with regard to the annual cycle of the swarming phase in the tropics, except that the swarms appear there at more or less definite seasons of the year, which suggests the existence of some fixed annual cycle.

Pairing and oviposition in temperate regions occur relatively late in the season, much later, for instance, than in the Moroccan Locust. The number of egg-pods laid by a female is not known exactly, but a very prolonged period of pairing and oviposition, extending sometimes over three months (Vinokurov, 1914), suggests that there must be repeated pairing and egg-laying by one female. Ecological conditions of oviposition have been described above (p. 243).

The eggs of the swarming phase hibernate in the soil, but cases of autumn hatching are not unknown (Dobrovolsky, 1921 ; Filipjev, 1926).

Hatching in the spring occurs at different dates and depends on the climate of the locality and also on the level of water in the rivers, on the shores of which the egg deposits usually are. Many are submerged under water during the spring floods, and it has been proved by numerous observations that temporary submergence does not affect the eggs, though the maximum period for which they are able to withstand submergence is not known. It sometimes happens that a deposit of eggs is flooded in spring and the water does not recede until the autumn, but it is unknown whether such eggs will be able to hatch in the following spring, if the level of the water then falls ; some Russian authors are inclined to think that a case of this kind may result in the hatching of locusts where eggs were laid two winters before.

The flooding of eggs has always the effect of retarding the hatching of hoppers and, if the infested area emerges from under the water gradually, the hatching may extend over a long time, a fact that much hampers control measures.

The behaviour of hoppers has been fully discussed in Chapter IV. It may be added here that the mass movements of the Migratory Locust differ

essentially from those of the Moroccan Locust and some other species, which depend mainly on the conditions of their habitat. The hoppers of the Migratory Locust, owing to the dense vegetation in their natural haunts, cannot form bands with a wide front, but are compelled to move in narrow but very dense and long columns along roads, paths, etc., amongst the reeds; wherever possible, however, typical bands with a broad front are formed.

As regards food plants, the Migratory Locust is not as omnivorous as it is often represented to be. Its staple food is reeds (*Phragmites communis*), other Graminaceous plants being of secondary importance. Mickelson (1922) stated that all plants of that family are eaten, without exception, while Maltzev (1915) successfully bred the locust in cages on absolutely dry hay, sprinkled with water. Plants of other families are also eaten, but in many cases it is difficult to decide whether they are devoured for food or for the sake of getting water, the need for which is very great in this locust (Nikolsky, 1925). Many of the plants recorded in the literature as subject to damage by the locust are eaten only after a period of starvation. According to Mickelson (*l.c.*), hoppers refuse to eat beans, cucumbers, lucerne, cabbage, sage (*Artemisia*), and Salsolaceæ; adult locusts will eat cabbage and lucerne, but very unwillingly. Migrating swarms, after a long flight, often damage various plants including even trees, but Nikolsky (*l.c.*) rightly says that this is not true feeding, since the locusts only nibble leaves and stalks, so that they often fall off; they do this for the sake of getting water.

The behaviour of flying swarms has been described in a previous chapter (see p. 85), and it may be added here that the migratory flight of this species is remarkable for its regularity and for the long distances covered. Another peculiarity is that the direction of the flight is generally speaking not accidental. Nikolsky (1925), who studied flights in the Syr-Darya region, states definitely that swarms there migrate from one breeding ground to another, the general direction of flights being upstream. On his observations he found it possible to evolve a general theory that the migrations of this locust lead only from one breeding ground to another, and not away from them. This theory is not supported by observations in other regions, though the general rule that migrations are often upstream holds good, as I have observed in the Caucasus, while Mr. B. Zolotarevsky writes to me from Madagascar that the same can be noticed there. The reasons for this curious regularity are quite obscure, and further studies on migrations are necessary before it can be explained; attempts to explain it on the ground of usefulness for the preservation of the species may be safely dispensed with, since they do not increase our knowledge of the fact and tend to obscure and prejudice the issue.

Periodicity

Extremely striking fluctuations in the numbers of the Migratory Locust, connected with mass emigration from the breeding grounds, has always attracted the attention of entomologists, and there is no lack of attempts at an explanation of this. While the general problems of periodicity have already

been discussed in a previous chapter (see p. 144), we will now merely see how the theory of periodicity based on phases can be applied to the Migratory Locust.

A difference between the Migratory Locust and the Moroccan Locust consists in the fact that the habitats of the solitary phase of the latter are very restricted and transformation into the swarming phase may occur partly, if not mainly, in the temporary and not in the permanent breeding areas (see p. 230). In the Migratory Locust, on the contrary, the solitary phase, *danica*, is very widely distributed, but the conditions for its transformation into the swarming phase exist only in restricted areas and not always even there.

It is often stated in a very general way that outbreaks of the locust follow very hot and dry years. If this were so, the outbreaks should occur, at least

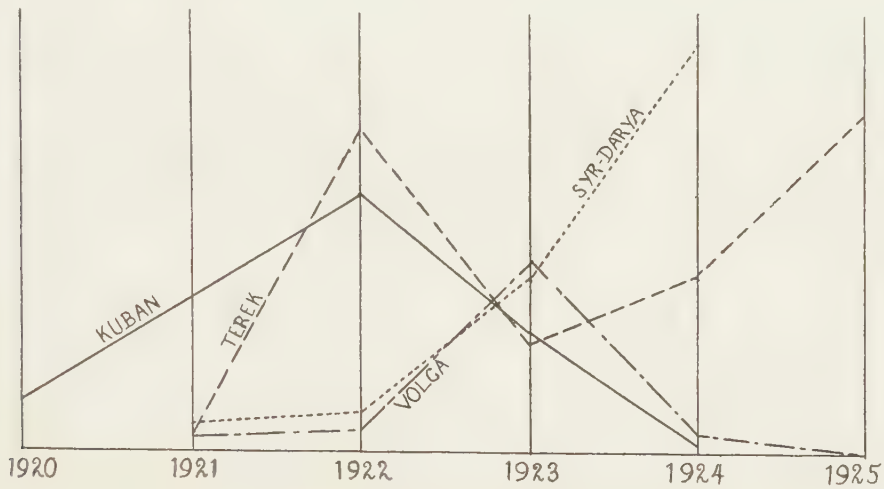

FIG. 87.—Fluctuations in numbers of the Migratory Locust in the chief permanent breeding areas of Russia for the period 1920–1925 (original).

in a single geographical area, more or less simultaneously, but this is not borne out by facts. Thus, for instance, the curves of the areas under egg deposits in Russia for several years (Fig. 87; based on data by Filipjev, 1926), show plainly that an increase of the numbers of locusts in different breeding grounds is not simultaneous. This implies that regularities in the fluctuation of numbers of locusts may be best observed when the study is restricted to definite grounds and no attempt is made to generalise at the outset.

The fact that climatic influences are acting differently in diverse breeding grounds may be due to special minor climatic conditions in each ground. If, for instance, a general rise of temperature in summer of 5° is sufficient to create optimum conditions for the locust in one breeding ground, it does not follow that the same will be the result in others, where a more open position, excessive moisture, etc., may be factors that render such a rise in temperature insufficient. If we also take into account that fluctuations of locust numbers are further affected by the activities of birds, parasites, fungous and bacterial diseases, etc., all these in their turn being dependent in varying degree on

climatic conditions, the enormous complexity of the whole phenomenon becomes obvious.

In any case, it seems highly probable that the first stimulus to an increase in numbers is usually given by optimum climatic conditions in a particular season. In tropical countries dryness seems to be the determining factor, while in temperate ones a high temperature is very important in this respect. An increase in numbers is followed by the appearance of the swarming phase, and the curve starts to rise suddenly. Then an emigration follows, and the breeding grounds remain, in most cases, almost free from the locusts. Migrating swarms may find (more or less accidentally) areas suitable for temporary breeding, but more often oviposition takes place under conditions very different from those in the breeding areas, which by reducing the numbers of the next generation, tend to influence a return to the solitary phase ; the activities of natural enemies naturally increase at this period and further accelerate the transformation.

The theory of phases helps us, in this way, to understand the process of periodic fluctuation, but does not explain its actual causes. These we may hope to reach only after detailed and extensive studies on the quantitative balance of locusts and their natural enemies in the breeding grounds in connection with the local and seasonal ecological conditions and with the morphological variations from one phase to another.

The Locust Problem in South Russia and in the Tropics

Amongst the tropical countries where the Migratory Locust occurs, it has, or had, most importance in Madagascar and the Philippines. As we know, however (see p. 239), swarms of this species have been known in West and East Africa, and there is no doubt that these countries sooner or later will experience the ravages of it. The Federated Malay States also cannot be considered safe from this locust, though many years have passed there without an outbreak.

In Madagascar the locust is very nearly a permanent pest, being particularly dangerous to rice fields and thus affecting the principal food supply of the natives. Although some measures against locusts have been adopted since 1915 (Institut Intern. Agriculture, 1926), they remain mainly on paper and have no influence on the pest. It is only since 1926 that an entomologist has been appointed to study the problem, and it is quite certain that many years will pass before an adequate organisation can be built up and practical results obtained. The general low standard of culture on the island, difficulties of communication, very sparse white population, etc., are all factors that hamper the establishment of an effective system of control. Under the circumstances it would be hopeless to attempt the immediate organisation of control on a large scale, and a more practical policy would be to concentrate on the defence of crops, while special attention should be paid to thorough investigation of the breeding grounds and bionomics of the locusts under local conditions, which are unknown ; these investigations will be of great help in the future when general conditions would permit a more extensive organisation.

The locust problem in the Philippines has apparently the same difficulties as in Madagascar. A good deal of work is being done there during outbreaks, but the usual wasteful and ineffective methods of ditches, burning, etc., are employed, while the labour is, of course, forced. Lately there have been some tests with aeroplanes for dusting, but apparently this was only done on an experimental scale. Theoretically, dusting with aeroplanes may perhaps be a very suitable method for use in very little cultivated countries like the Philippines or Madagascar.

The Migratory Locust is of exceptional importance in certain years in Russia. Normally, when the locusts are confined to their breeding grounds, their importance is very small, since in most regions these are surrounded by uncultivated land and stray bands of hoppers coming from reed beds can do no harm. It is when an emigration takes place that the position becomes very serious. The emigrating swarms themselves are not very dangerous since the locusts at this period eat very little (see p. 87), but the eggs are usually laid in cultivated lands, often actually amongst crops, since this species prefers to oviposit in soft soils. Periodic migrations of swarms from now non-existent breeding grounds on the lower Danube, Dnieper, and Don were for many years a hindrance to the successful colonisation of the South Russian steppes, and at present similar conditions still exist in the Northern Caucasus and in Turkestan. Russian entomologists, however, have long been aware of the necessity for undertaking full responsibility for the anti-locust work, and its organisation has been in their hands for a long time ; they also have done their best to suppress the system of forced labour and, as a result, a solution of the locust problem was definitely in sight just before the Great War. The revolution, however, destroyed the results attained to such an extent that certain breeding grounds that had been considered extinct began to function again. There is, nevertheless, a definite policy of controlling the Migratory Locust in its permanent breeding grounds, new methods (notably dusting from aeroplanes) are being introduced, and research work is being carried out on a large scale.

CHAPTER XII

THE DESERT LOCUST (Schistocerca gregaria, Forsk.*) AND THE LOCUST PROBLEM IN NORTH AND EAST AFRICA AND IN WESTERN ASIA

Description of Stages

Adult of the Swarming Phase (ph. *gregaria*, Forsk.) (Fig. 72).—Large. Pronotum very distinctly constricted in front of the middle, in profile straight; surface almost smooth; hind angle broadly rounded; metazona (*i.e.* the part behind the hind transverse sulcus), broader than long; colour uniform, without dark pattern. General coloration yellow (when sexually mature) or pink (recently moulted into the adult stage), with small dark spots on elytra. Hind femora unicolorous; hind tibiæ yellow, spines black on the tips. Prosternum (between the bases of the front legs) with a straight spine with its apex rounded. Male genital plate with a triangular excision at the apex; male cerci compressed laterally with the apex slightly emarginate. Length, male 46–55 mm., female 57 mm.; elytra, male 50–60 mm., female 60 mm.

Adult of the Solitary Phase (ph. *flaviventris*, Burm.) (Fig. 72).—Differs from the swarming phase mainly in coloration and in the structure of the pronotum. The latter is more elongated; median keel more distinct; metazona about as long as broad; hind angle straight, scarcely rounded. General coloration of freshly moulded adults greenish-white; sexually mature adults yellowish-grey, with dark stripes on the pronotum and a pale stripe along its middle.

Hopper of the First Stage † (Fig. 88; Plate IX, Fig. 1).—Blackish-brown. Head with some yellowish spots and with a fine pale median line which is continued on to the pronotum and abdomen. Sides of pronotum with bow-shaped yellowish spot. Hind femora with three paler spots. Length at the beginning of the stage 8 mm., at the end 12 mm.

Hopper of the Second Stage (Fig. 88; Plate IX, Fig. 2).—Similar to the preceding stage, but the pattern more distinctly defined and the darker parts becoming black, while the paler ones are yellow or pinkish. Length at the beginning of the stage 12 mm., at the end 18 mm.

Hopper of the Third Stage (Fig. 88; Plate IX, Fig. 3).—Face and base

* The name Desert Locust is proposed here for the first time and is chosen because of the habitat of the species. Latin synonyms of the species are: *S. peregrina*, Ol.; *S. tatarica*, auct., nec L.

† There are no good morphological descriptions of hoppers of various stages; my descriptions are based mainly on those by Vosseler (1905), by Regnier (1926), and figures by Künckel.

of antennæ pale orange. Semilunar pronotal spot becomes broader. Abdomen yellow or pink, with numerous blackish dots, and series of black spots along the middle. Rudiments of elytra and wings distinct, black. Hind femora fasciated with black and pale. Length at the beginning of the stage 17 mm., at the end 25 mm.

Hopper of the Fourth Stage (Fig. 88; Plate IX, Fig. 4).—General coloration rose or lemon-yellow; black pattern very strongly pronounced. Bow-shaped spot on the pronotum becomes more narrow. Rudiments of elytra and wings pale, turned up on to the back. Abdomen with sharply defined broad median stripe. Length at the beginning of the stage 25 mm., at the end 33 mm.

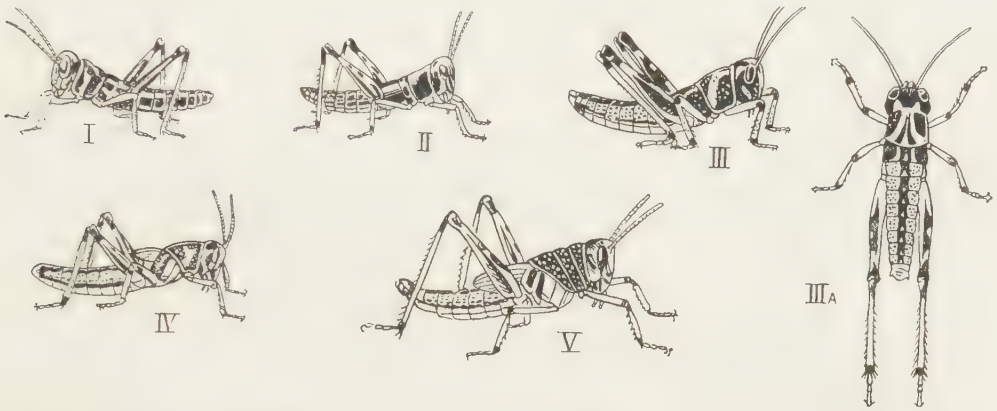

Fig. 88.—Hoppers of the Desert Locust; the stages numbered; hopper of the first stage more, that of the fourth less, enlarged than the others (after Künckel).

Hopper of the Fifth Stage (Fig. 88: Plate IX, Fig. 5).—General coloration yellow, or orange-yellow; black pattern either becomes reduced or else (in East African individuals) extended. Pronotal spot in any case losing its definite outline, or even disappearing. Length at the beginning of the stage 33 mm., at the end 38–45 mm.

Hoppers of the Solitary Phase (Plate IX, Figs. 1*a*–5*a*).—Coloration (in the later stages) pure green, or with traces of black markings (Johnston, 1926).

Egg-pod (Fig. 42, S).—External envelope very thin and fragile, especially towards the time of hatching, when it is impossible to find whole egg-pods. The upper part of the pod has a stopper, made of porous material, about 3–4 cm. long. The number of eggs varies from 40 to 90, and they are not arranged in rows, as in other Acridids, but lie irregularly in the pods. Egg about 8 mm. long and 1–1·2 mm. in diameter; its surface with hexagonally arranged ridges.

Distribution and Ecology

The Desert Locust has a very wide area of distribution in the Old World (Fig. 89), both in the solitary phase and in the swarming one, though the information at hand is far from being exhaustive and in certain cases not quite reliable owing to frequent confusion with other species. Similar confusion has also occurred with the South American Locust, and old writers

have stated that the same species of *Schistocera* occurs both in the Old and the New World, but this is erroneous (Uvarov, 1923 ; see also Chapter XIII).

In Africa the general area of distribution of the Desert Locust covers very nearly the whole of the continent, with the exception of more humid and heavily wooded tropical regions of West and Central Africa.

It is in the North-West of Africa—that is, in Morocco, Algeria, and Tunis —that this locust is particularly well known for its periodic ravages. The history of the invasions (not only of this species, but also of the Moroccan

FIG. 89.—Area of distribution of the Desert Locust (original).

Locust) has been collected in the enormous work by Künckel, but unfortunately there is very little information in it that might be of real value for the study of the bionomics of this locust. It is assumed that the Desert Locust does not breed normally anywhere near the cultivated zone of North-West Africa, but that its swarms arrive from the Sahara ; some authors even ascribe the source of the swarms to Senegal and the Sudan, but this would involve the necessity for swarms to cross the whole Sahara on their migratory flights, and it seems very doubtful whether this is possible. On the other hand, there are already records (Uvarov, 1923) of the occurrence in the Algerian Sahara of the solitary phase, and this makes it permissible at

least to suggest that the permanent breeding of the locust may be possibly in the Northern Sahara, quite close to the Atlas mountains. In making this suggestion I do not deny that some swarms may possibly originate farther south, in the central parts of the Sahara, but merely wish to draw the attention of local entomologists to the possibility of discovering breeding areas much nearer at hand than they are usually supposed to be.

As is only to be expected, there are absolutely no ecological data on this locust in North-West Africa, and the available information on the conditions of egg laying by swarms refer to insects that have migrated and cannot be considered as illustrating the normal ecology of the species.

Eastwards, the Tunisian area of the Desert Locust extends into Tripolitania, where also no information exists as to the source of locust swarms that appear from the desert.

Northwards the locust extends into the Iberian Peninsula, where it has been known more than once from the extreme South of Spain and particularly from Portugal, but it seems certain that in all cases the appearance of the locusts has been due to stray swarms from Africa, and there is no reason to suggest the possibility of local breeding.

The data on the distribution of the locust south of the Sahara, in Senegal and the French Sudan, are very confusing. While numerous records exist of devastations caused by "locusts," it must be remembered that they have emanated from officials having no knowledge of entomology and, even in cases when a specific name is given, it must be accepted with great caution. There is no doubt that in many instances swarms of another species, the Tree Locust (*Anacridium moestum melanorhodon*, Walk.*), were erroneously recorded as those of the Desert Locust. Vayssière and Mimeur (1925) state that all swarms of locusts that were observed by the second author in French Equatorial Africa in 1922 and 1923 consisted of *Anacridium*, not of *Schistocerca*. This, of course, does not mean that the latter species does not exist, or does not swarm there, but merely emphasises the necessity of more exact studies on the local species. Personally I am fully convinced that the Desert Locust exists in the whole wide belt of the drier steppes bordering on the Sahara from the south and extending right across the African continent. It may be added that there exist definite records of *Schistocerca* from Senegal and the French Sudan (Vayssière and Mimeur, *l.c.*), though whether from swarms or not is unknown.

It is only at the other end of the belt just mentioned, in the Anglo-Egyptian Sudan, that the situation with regard to the locust in question is clearer than in other parts of Africa owing to the recent work of Johnston (1926). Here it was usually assumed that locust swarms arrive from the deserts, where in some very remote parts there are special breeding grounds. This has proved to be not correct, since the presence of the solitary phase (*flaviventris*) has been definitely proved in many places within the Sudan itself; moreover, a case of incipient swarming came under direct observation,

* This locust is very similar superficially to the Desert Locust, but can be distinguished at once by the presence of a smoky band on the hind wings (see p. 319).

and this all indicates that breeding of this locust in the solitary phase is possible throughout the Sudan with the exception of the more humid southern provinces, and that the transformation into the swarming phase may also occur locally if the conditions are favourable. Of course, this does not mean that the solitary phase is quite generally distributed regardless of ecological conditions ; on the contrary, there are reasons for thinking that it has definite ecological requirements. Johnston considers the typical breeding country for the species to be sandy desert with scattered scrub (information kindly communicated to me, but not yet published ; see Plate VIII, Fig. 1).

North of the Sudan, the locust is known from Egypt, but its swarms are not always of local origin, and arrive from the adjoining deserts, though probably not from as far as is supposed.

In the equatorial parts of East Africa the locust occurs in British East Africa and in the former German East Africa (Vosseler, 1905 ; Morstatt, 1921). According to Morstatt, the species occurs singly (probably in the solitary phase) as well as in swarms, and this indicates that the swarms are due to local multiplication and to transformation into the swarming phase, not to a migration from long distances.

Farther south, no information exists on the locust as a pest. There are, however, numerous records of both the solitary and swarming phases from the Cape province and South-West Africa (Uvarov, 1923), and it seems fairly certain that the species has always been confused by local entomologists with other locusts.

Turning our attention to Asia, we find that the Desert Locust seems to be a regular pest in Arabia, but no information of any value exists with regard to that country. Invasions of swarms of this species are also known in Palestine (Bücher, 1918), and their source is usually assumed to be Egypt ; though some swarms may come across the Red Sea and the Sinai desert into Palestine, there is also a possibility that the locusts arrive in the latter country from some relatively near places in Arabia and, perhaps, even from the southern parts of Palestine itself. In any case the climatic conditions of Palestine are scarcely favourable for the permanent breeding of the species, and its solitary phase has not been found there.

Farther eastwards, the Desert Locust breeds in Persia, Baluchistan, and the Punjab. There is no reliable information as to the main breeding areas in Persia, but during the latest outbreak (still in progress at the time of writing) considerable swarms were breeding as far north as the Khorasan province, while stray specimens are known from Russian Transcaspia. With regard to Baluchistan, Webb Ware (1915) insists that the locusts there are not local, but arrive from Persia, and he locates the breeding grounds in the Kirman desert of Persia ; whether this is always the case, is not clear, but in any case the Desert Locust can breed in Baluchistan for several years, if not permanently. In the Punjab the locust can breed also, at least temporarily, and the following description of the breeding grounds by Moore and quoted by Cotes (1890) is undoubtedly the best :

" The locusts breed in the most sandy and desert districts of Rajputana,

especially in the *taburs* or sand-hills of South-Western Manour and Mullanni. The locality mentioned presents a succession of sand-hills from 50 to 200 feet high and some miles long. As a rule they run in a south-easterly direction. This remarkable tract extends over thousands of square miles, commencing near the Runn of Cutch, and forming a broad belt of country towards Bhawalpur and Bikanir. During the monsoon season, it is fairly green from the growth of a species of *Mimosa* on which the camels feed. At other periods it presents a bright blinding whitened appearance."

During the latest (1926–27) invasion in Sind, Kathiavar, and Gujarat, the hoppers of the Desert Locust were observed in the sandy bed of the river Hab, near Karachi, while other breeding areas in the Sind-Rajputana desert, though not definitely known, must also exist (Mann and Burns, 1927) and can even reach as far as Assam (Andrews, 1915).

Summing up all this meagre information on the distribution of the species, we can see that it is definitely connected with dry desert and semi-desert regions. Our knowledge of its ecology does not go beyond the vague indications that breeding is connected with sandy areas.

Bionomics

Of the bionomics of the Desert Locust very little is known. To begin with, the important problem of the number of annual generations is solved by different authors in a variety of ways, but all suggestions put forward have one point in common, in that they are all rest on fragmentary evidence and theoretical assumptions, not on continuous direct observations throughout a season.

Künckel was inclined to think that in Algeria there are two generations a year: swarms arriving from the Sahara in winter in an immature state (pink coloured) reach maturity and lay their eggs in spring; hoppers from them hatch within a few weeks, and new swarms, immediately on becoming winged, migrate back into the Sahara, where they produce another generation, and this invades Algeria again. Vayssière (1921*a*) offered another suggestion, based on an analogy with *Schistocerca paranensis*, namely, that the swarms produced in Algeria migrate into the Sahara, hibernate there in a sexually immature stage, and invade Algeria again; thus, only one generation exists, but with a very prolonged imaginal diapause (see p. 50). While this second suggestion seems more reasonable than the first, it cannot be accepted without corroboration by direct observations.

In the Sudan the data as to the number of generations are also insufficient; King (1922) is inclined to admit only one, and he believes that at the end of the season the swarms do not migrate into the deserts, but break up and lead more or less solitary lives as scattered individuals until the atmospheric or other conditions cause them to re-acquire gregarious habits. The weak spot of this suggestion is the necessity for admitting a double change in the behaviour of locusts from swarming to solitary and back again, but this is not impossible, and the theory deserves close investigation.

In Northern India, Cotes (1891) records some evidence showing that

oviposition can sometimes occur within fairly short time after the locusts have acquired wings, *i.e.* without a long diapause, and he is inclined to think that, at least in some cases, the locust is able to produce there more than one generation a year. His data show also that the egg-laying period may extend over several months and that an overlapping of generations produced by different swarms may result, which complicates the matter still more.

It is impossible to arrive at a definite conclusion based on such unsatisfactory evidence, and only future direct observations will settle the problem. When comparing the observations, it must not be forgotten that the annual cycle of the swarming and the solitary phase may be different, as is the case with other locusts. It seems probable that the swarming phase has really only one generation a year, while the solitary one may have more.

As regards development, the salient point is the practical absence of the diapause in the egg stage, since the eggs hatch in 16–40 days, though in exceptional cases the embryonic period may extend to 70 days. The duration of the larval period is about 40–50 days. The hoppers are markedly gregarious in their habits, and begin their mass wanderings very early, and larval bands reach an enormous size.

The feeding habits are not sufficiently well known, since most authors simply record damage to crops in a general way. Künckel, however, gives interesting lists of wild plants eaten and avoided by the Desert Locust ; the second is actually far longer than the first, and it includes, apart from numerous Salsolaceæ and similar plants of peculiar taste or smell, several Gramineæ (a puzzling feature of the lists being that some plants are included in both, which may, perhaps, mean that they are eaten only occasionally).

Mann and Burns (1925), after observations on flying swarms in Sind, recorded that *Tamarix*, *Acacia arabica*, *Prosopis spicigera*, *Calotropis gigantea*, and a few other plants are not damaged, while *Capparis aphylla*, *Casuarina* trees, and some others, as well as all standing crops, suffered heavily.

Migrations attributed to this species by Künckel and other authors are remarkable for their extent and regularity, but it must be admitted that most data on the subject are either fragmentary or unreliable. The northward migration of winter swarms in Algeria has been observed better than in other cases, and it is remarkable that the swarms undertake a series of flights, stopping at different places and then continuing again. On the contrary, with regard to the summer swarms it is stated that they migrate immediately and fly off without stopping into the Sahara. An analogous disappearance of recently winged swarms is also recorded by Vosseler in East Africa (1905), but it is uncertain whether the swarms actually fly far, or whether they simply scatter as King (1922) has suggested.

Yet another very important point in the bionomics of the locust is the number of egg-pods laid by one female. Künckel, on observations in cages, was ready to admit as many as eleven successive ovipositions, but it is scarcely necessary to dispute this statement. Vosseler (1905) regards two ovipositions as not impossible, but he failed to obtain any definite evidence. Field

observations on repeated egg-laying by one swarm have been made more than once, but they are of little value, since there is no proof that the eggs were laid on different occasions by the same females ; it is more likely that the females do not all become mature simultaneously, and in this way the period of oviposition of the whole swarm may be extended.

Periodicity

Johnston's observations in the Sudan established the connection between the periodic swarming of the Desert Locust and its phases (see p. 157), but they only showed the way for future research, which must be particularly directed to finding out the conditions that produce the initial increase in the numbers of locusts, an increase that is followed by transformation into the swarming phase. According to Johnston, this may be due to exceptionally heavy rains in winter causing the appearance of vegetation in the desert, but the whole problem awaits thorough investigation.

The Locust Problem in North-West and East Africa and in Western Asia

There is little doubt that in respect of its destructiveness the Desert Locust deserves the first place amongst the locusts of the Old World, the history of its ravages reaching as far as there is any historical evidence at all. With full justification this species could be called the Bible Locust, since the numerous allusions in the Bible to locusts are practically all based on *Schistocerca* (partly, perhaps, also on the Moroccan Locust, which is not unknown in Palestine). At present a new invasion of the Desert Locust is beginning all over the area of its distribution.

This history of the locust in Algeria and Tunisia is set forth in Künckel's voluminous work, but we will not waste time on recording information of purely historical interest and will turn our attention to the present situation.

As stated above, the locust in Algeria is not considered to be a species that breeds locally, but a periodical intruder from the Sahara desert. I do not think, however, that these mysterious haunts of the locust in the desert are really so far removed from the cultivated zone as they are supposed to be. Indeed, the solitary phase of the species has been actually found at Ain-Guettara (Uvarov, 1923), and this shows that the species can survive during the periods of minimum in the Northern Sahara without necessarily migrating into its central parts.

The periodical ravages of the locust especially in Algeria are enormous, and the causes are not difficult to see. In the first place, the bionomics of this species have a very unpleasant correlation with the local agricultural conditions. The invading swarms are recorded to be doing great damage, because they appear in the early spring when the field crops are green ; the rapidly succeeding generation of hoppers is again in time to feed on the same crops and on those appearing a little later. Thus, the whole harvest of the year may be destroyed, while the locusts, both in the hopper and the adult stage

also feed on vegetables, garden crops, and even vines ; the damage to orchards and vineyards is, of course, particularly heavy, owing to the value of these crops.

Another reason for the seriousness of the locust problem in North Africa is the difficulty of organising campaigns on a really effective scale, coupled with the eminently unsatisfactory technique and organisation in use. Indeed, the basis of the anti-locust work is legislation, providing for a compulsory control of locusts by peasants and landowners. By the laws in force in Algeria, for instance (Institut International d'Agriculture, 1926), the State only provides the necessary apparatus and materials, and neither the central Government nor its local representatives are supposed to take an active part in the control work, which is presumably carried out by the, so-called, obligatory " syndicates de defense," or simply by landowners and peasants compelled to organise fighting groups. Thus, there is no united organisation for the whole country, no expert leadership of campaigns, and the actual work is permitted to be done by any technical methods that satisfy the purely formal requirements of the law. The methods in use are partly barriers (used mainly for the passive protection of crops) or insecticides (cresyl), but apparently are mainly the time-honoured ones such as ditches, collection of eggs, and others equally futile. Poison baits are now being introduced, but on a very small scale, and their use, as is also the case in Morocco, is strictly regulated by laws applying to the use of internal poisons.

It is therefore not surprising that the locust invasions in Algeria and Morocco usually last as long as they might be expected normally to do without interference on the part of man, and the net result of the campaigns (if so they may be called) is only the saving of some fields and gardens from immediate destruction, while no attempt is even made towards actually controlling the locusts.

A " regional anti-locust station " has been founded in Algeria with the object of collecting information on movements of locusts in all North African countries and passing it on to the countries concerned, but its activities are again of merely defensive value, while it is not even intended to do anything in the way of studying the locust problem or attempting to consolidate control measures in all North African countries. Indeed, from what has been made known so far of the activities of the Station, they consist in receiving telegraphic communications on movements of swarms and sending them on to other countries for information. Work of this kind is necessary, but only when every country concerned has a really effective control organisation. In present circumstances the usefulness of this Station seems very questionable.

The ineffectiveness of the Algerian organisation is clearly demonstrated by the fact that the last invasion of the Moroccan Locust started in 1920 and was still in progress in 1927 in spite of heavy annual expenses on the part of the Government (for apparatus and materials) and an enormous amount of work done by the population. There were no invasions of the Desert Locust within that period, but some swarms appeared in 1927 announcing the beginning of a new outbreak, and it may be feared that an organisation that

is ineffective against the Moroccan Locust, which is relatively quite easily controlled, will be absolutely useless against the Desert Locust.

Practically identical is the situation in Morocco (where, however, a central organisation has been established quite recently, and a locust research laboratory started its work); still worse is it in Tunisia and Cyrenaica, where no outbreaks of locusts have occurred within recent years and, consequently, no actual preparations are considered necessary to meet future invasions.

The road to improvement in North Africa is clear, and it must be taken immediately, without waiting for a new outbreak of *Schistocerca*, which seems to be on its way. First and foremost, the principles of the organisation of control must be revised drastically in favour of centralised campaigns with entomologists at their head, acting not merely as advisers, but as responsible leaders. Secondly, the methods of control must be standardised, and the campaigns based on barriers and poison baits; the use of the latter should be facilitated by removing absurd restrictions against arsenic; methods like the collection of eggs and ditching must be abandoned entirely. Finally, active work on studying local locust problems must be started on a sufficiently large scale, since the present state of our knowledge leaves us in the dark as to the most important points of immediate practical interest (breeding areas, number of generations, etc.). On this basis, together with the co-operation of all countries immediately concerned, a very effective system of control can be built up, but of course of a primarily defensive character. To carry the work still further—that is, to endeavour to prevent outbreaks—would require first of all a better knowledge of local conditions and of the bionomics of the locusts involved than we possess at present, and it would be premature to discuss this aspect of the problem in respect of North Africa.

In French Equatorial Africa the locust problem is still at such a stage that it is difficult to discuss improvements in the organisation. There is, apparently, no definite system of locust control, and most primitive methods of combating locusts are taken by the natives under compulsion from the administration when it is absolutely necessary. A special service of collecting information on movements of swarms throughout the country has been established since 1920 (Institut International d'Agriculture, 1926), the data being conveyed to the Algerian Regional Locust Station. A fairly large amount of data has been obtained (apparently through native chiefs and local administrations), but the whole of the information is actually valueless, since the species of locusts involved is not stated, whereas several are present in the country. Until the general entomological service in the country is developed on a sufficient scale, it is impossible to expect any practical results from the existing attempts at locust control.

The locust problem in the Anglo-Egyptian Sudan is a serious one, and is due, apparently, only to the Desert Locust (King, 1915; Johnston, 1926). It is true that the last period of activity of this locust ended in 1917, and no invasions of a serious nature have occurred since then, but in 1926 an incipient outbreak was observed (and suppressed) near the Red Sea coast, and this seems to indicate the beginning of a new period of ascendancy of the locust,

the more so that the latter is on the increase in other parts of its area as well (Persia, Baluchistan). The economic status of crops in the Sudan at present, with the area under cotton increasing every year, is very great and growing annually, so that an invasion of locusts now would mean infinitely more than it did ten years ago. It is, therefore, with a great satisfaction that we are able to record conditions in the Sudan that make the prospect less gloomy than they might be. Indeed, even at the time of the last outbreak the technique of control by means of poison baits was tested, found eminently satisfactory, and applied on a large scale. There also exists an entomological organisation of sufficient capacity to deal with the locust problem, or, at least, to become a nucleus for an effective and extensive anti-locust organisation. Finally, the first step towards the elucidation of the mechanism of periodicity of the locust has been made in the Sudan (Johnston, 1926), and it leads to some practical suggestions of great value.

Johnston's observations (see p. 157) have shown that locust outbreaks in the Sudan may develop on the spot from individuals of the solitary phase transforming into the swarming one under favourable conditions ; they have proved, also, that such incipient outbreaks can be dealt with very easily and at a small cost and suppressed before assuming dangerous proportions. Thus, the problem of preventive control of locusts in the Sudan would consist in locating the places where the locust can breed in the swarming phase and organising a permanent observation on them. The first step would be, therefore, to study extensively and thoroughly the ecological conditions of life of the solitary phase and of its transformation into the swarming one. Johnston's work has shown the way to doing this, but further investigations in that direction have, apparently, stopped, since the immediate danger from locusts was removed. This is a mistake that may result in most disastrous consequences. Investigations of this kind cannot be completed in a year or two, but must be extended over a considerable period and over the whole country ; it is, therefore, a short-sighted policy to stop them simply because there is no immediate danger from locusts, since it will be too late to resume them when the locusts appear. There can be no doubt at all that locusts *will* appear in the Sudan, and it is only a question of time. An immediate start on the investigations of ecology and bionomics of locusts would be the best step in the direction of the prevention of an outbreak, and it is to be hoped that this will be made without delay.

In Egypt the locust problem, as such, scarcely exists, invasions being very rare, and the last one has shown that the dense population concentrated on a relatively narrow strip of cultivated lands in the Nile valley is perfectly able to deal with invading swarms with some technical assistance from the Government.

South of the Sudan, in the East African colonies (Kenya, Uganda, and Tanganyika Territory), the Desert Locust is of rarer occurrence, but this seems to depend to a large extent on the relative smallness of areas under cultivation, and future outbreaks of locusts will certainly be of far greater economic importance than in the past ; in other words, the locust problem there may be said

not to exist to-day, but it will undoubtedly emerge at some not very distant date. It would be, therefore, not too early to begin investigations on locusts in those countries now.

While I have reasons to think that the Desert Locust may swarm occasionally in some parts of South Africa, where it must have been confused with more common species, there is no doubt that the real locust problem is there caused by the Brown Locust, and it will be more convenient to discuss the situation in the chapter on that species (see Chapter XIV).

As regards Asia, the locust problem is very grave in Palestine and Transjordania. The invasions there are relatively rare, it is true, and the locusts can get no firm footing in the country owing to unsuitable conditions, but the economic basis of the country rests on its intensive cultures of olives, vines, etc., so that the losses even from a single locust swarm may be enormous. At the same time, there is scarcely any possibility of contemplating measures for the prevention of locust invasions that originate outside the country, in Arabia, or in the southernmost parts of Palestine which are practically devoid of population. This makes it the more necessary to take precautions for meeting the danger, when it comes, in the most effective way. To ensure this, some system of observations on the probable breeding areas is necessary so that a warning can be given of incoming swarms ; apart from this, a sufficient amount of materials for the control on a large scale must be kept ready even if there is no immediate danger.

There is not much to be said on the locust problem in other Asiatic countries. In Iraq, Transjordania, Persia, and Baluchistan, to say nothing of Arabia, the extent of cultivated areas in proportion to waste land is far too small to expect any really effective organisation of locust control. The most that can be attained there is the successful defence of crops during invasions, and this, I firmly believe, can be accomplished even there, provided that poison baits are made the basis of the technique and the organisation centralised and led by entomologists ; above all, the minor administrative officials must be absolutely eliminated from the control organisation, since it is notorious that anti-locust campaigns in those countries are regarded by them as a source of income owing to the practice of conscripting labour.

The situation in North-Western India, where the locusts appear only occasionally, is none the less very serious since this irregularity of locust attacks there accounts for an absolute absence of any organisation capable of dealing with them. This was very convincingly demonstrated during the invasion of 1926–27, when it was found difficult even to collect information on the movements of swarms, etc., to say nothing of active control measures. The situation was summed up by Mann and Burns (1927) as " the general helplessness of the population due to lack of information regarding swarms and of organisation to deal with them." The same authors lay emphasis on the fact that the problem cannot possibly be dealt with locally, and suggest the necessity for a centralised organisation.

CHAPTER XIII

THE SOUTH AMERICAN LOCUST (Schistocerca paranensis, Burm.) AND THE LOCUST PROBLEM IN SOUTH AND CENTRAL AMERICA

Taxonomy of the Species

Many of the older writers assumed that the locust of South and Central America does not differ specifically from the Desert Locust of the Old World (*Schistocerca gregaria*, Forsk.), and even Scudder in his monograph of the genus (1899) referred some of the South American specimens to the last-named species. More recent research, however, has proved definitely that *S. gregaria* does not occur in the Western Hemisphere at all, and all records from there must be referred to another, purely American species, very similar to *gregaria*, but differing from it in a number of constant morphological characters (Uvarov, 1923; Hebard, 1923, 1925*a*). The problem of the systematics of the American Locust has not, however, been settled by this fact, since the genus is represented there by a large number (about eighty) of nominal species, and quite a number of them have been recorded by different authors as gregarious and migratory. While the majority of the records may be rejected, since the specific names quoted in them are not the result of serious systematic studies but of haphazard determinations by non-specialists, there still remain several species that are regarded as true locusts. Here belongs, first of all, *S. paranenis*, Burm., the species which is most often quoted as the true South American Locust. Another closely allied species, *S. pallens*, Thunbg., has been often recorded as the migratory locust from various countries in South America and the West Indies. Lynch Arribalzaga, after studying specimens of migratory locusts from Peru and from Trinidad, Colombia, and Venezuela, referred them respectively to two new species, *S. peruviana*, L. Arrib. (Lynch Arribalzaga, 1903) and *S. urichi*, L. Arrib. (1918). Finally several authors (doubtfully competent to decide such systematic questions) have referred to the South American Locust as *S. americana*, Drury.

Thus, it might appear that South and Central America are subject to ravages from several different species of locusts, which are, however, all very closely related to each other and differ mainly in colour characters and details of pattern. This seems highly improbable, and doubts as to the validity of the species involved have been expressed by some authors (particularly by Lahille, 1920), and they are inclined to think that only one species of *Schistocerca* is a true migratory locust in South and Central America and West Indies. Hebard (1923), while showing that *S. urichi* is a pure synonym of *S. paranensis*, is of the opinion that the last-named species is the true American migratory locust. I might add that *S. peruviana* differs from *S. paranensis* only

in some colour characters, and that the species seems to be founded on unusually pale specimens of that species. On the other hand, Hebard (1923) stated that *pallens* in some of its varieties is scarcely distinguishable from *americana*. If we admit (I am unable to express a definite opinion on the subject) that *pallens* does not differ from *americana* specifically, there remain only *paranensis* and *americana*. These two insects are undoubtedly not identical; they differ not only in colour, but also in some morphological characters, but it is a remarkable fact that their differences are very much of the same kind, as those between *Schistocerca gregaria* and its solitary phase—*flaviventris* (see p. 156). It is, therefore, not impossible that *paranensis* is but the swarming phase and *americana* the solitary phase of the same species. This view has been expressed recently by Dampf (1925), and we will return to it later when discussing the periodicity of the locust. At present, it is sufficient for our purpose to state that everything points to the existence in South and Central America of only one species of migratory locust, which may be tentatively called *S. paranensis*, Burm. If *S. americana* proves to be really only a phase of the same species, the latter name should be applied to it, and *paranenis* would be used for the swarming phase only.

I wish to emphasise that the above views are based largely on theoretical assumptions and, while I firmly believe them to be correct, it is absolutely necessary to settle the problem of the systematics of the genus *Schistocerca* definitely by the study, not of casually collected specimens from different localities, but material in really large quantities collected both from swarms and singly. From what we know about other locusts (*Locusta migratoria*, for instance, see p. 148), their ability to produce temporary phases strikingly different in appearance is coupled with a mass variation of whole swarms in one direction; therefore, by examining a series taken from one swarm, it is easy to find certain characters constant for the series and mistake them for specific ones; this mistake can only be avoided by studying the characters of the species on a mass of material taken from several swarms and singly during a series of years. This has never been done, and the result is an enormous confusion in the systematics of this important genus. It is abundantly clear that studies in the systematics of *Schistocerca* must be the first stepping-stone to a full understanding of the locust problem in the New World. In these studies an important point that must not be missed is the necessity for experimental work on the forms studied, since only then can their inter-relations become clear; in other words, the work must not be based only on museum specimens, however large series may be accumulated for the purpose, but on living material both in the field and in the laboratory.

For practical purposes, and only for the lack of better knowledge, we will accept the name *Schistocerca paranensis* for the locust we are now going to describe.

Description of Stages

Adult Insect of the Swarming Phase (*S. paranensis*) (Fig. 90).—Antennæ of the male about one-fourth longer than head and pronotum together. Pronotum conical, narrower in front, feebly constricted before the middle; its

metazona (the part behind the hind furrow) not broader than long. Elytra extending well beyond the hind knees. Subgenital plate of the male with the apex excised, but its angles rounded ; male cerci emarginate apically. The colour of the same individual varies according to the season, as follows (Bruner, 1898) :

Newly-winged Individuals.—Ground colour reddish ; a narrow pale stripe above on the head and pronotum, included between two slightly darker lines ; sides of pronotum with a large dark spot in the anterior half and a whitish narrow stripe in the middle of the spot ; lower margin of the sides of pronotum pale. Elytra greyish-white with fairly large blackish spots ; front margin whitish. Wings hyaline. Legs reddish ; hind femora on the outer side darker above than below ; hind tibiæ reddish ; their spines white, with black tips.

Wintering Individuals.—The contrasting dark and pale markings almost or quite disappear, the whole insect assuming a uniform dull-reddish or even brown tinge. The hind wings become a beautiful rose colour, more pronounced near the base of the wings.

Fig. 90.—South American Locust, female ; slightly enlarged (original).

Sexually Mature (*Spring*) *Individuals.*—The reddish colour gradually gives way to a lighter shade. By the time of egg-laying, the insect becomes yellowish-olive, with the wings yellowish-hyaline.

Length, male 48–52 mm., female 55–60 mm. ; elytra, male 46–52 mm., female 53–60 mm.

Adult of the Supposed Solitary Phase (*S. americana*, F.).—Very similar to the preceding. Pronotum without constriction, simply narrowed forward, with the metazona relatively narrower. Colour pattern more pronounced.

Hopper of the First Stage (Fig. 91, 1).—Antennæ 13-jointed. Dull greyish-brown ; sides of pronotum and metanotum, indefinite bands on hind legs and a stripe along the back very dark, sometimes even black. Length 7–9 mm.

Hopper of the Second Stage (Fig. 91, 2).—Antennæ 17-jointed. General colour lighter than in the first stage, being yellowish-grey, and the markings better defined. The dark line along the back sharply defined and bordered on each side by a lighter line. Hind femora with two bands, and the knees black. Face black. Sides of the abdomen with wavy lines of dark-brown and yellowish-grey. Length 10–12 mm.

Hopper of the Third Stage.—Antennæ with 20–22 joints. Rudiments of elytra and wings distinct, directed downwards. General colour yellowish; face, sides of pronotum, and bands of hind femora jet-black; other markings reddish-brown. Length 18–20 mm.

Hopper of the Fourth Stage.—Antennæ with 24–25 joints. Rudiments of elytra and wings turned on to the back, large. General coloration brighter

Fig. 91.—Hoppers of the South American Locust.—1, end of the first stage, × 4.—2, second stage, × 4.—3, fourth stage, bred singly, × 2·5.—4, third stage, typical solitary form, × 2·5 (after Dampf).

than in the preceding stage; brown markings on the abdomen become blackish-brown; eyes and the head above brick-red. Length 26–30 mm.

Hopper of the Fifth Stage.—Antennæ with 26 joints. Rudiments of wings reaching the end of the second abdominal segment. Coloration, as before. Length 35–40 mm.

Egg-pod.—There is no regular egg-pod in this species, the external envelope

being extremely thin and fragile so that the whole group of eggs cannot be taken out of the hole. The mass is 6–7 cm. long, a little curved, and its upper half, or a little less, is occupied by the stopper. Number of eggs varies from 51 to 120, and they are arranged regularly.

Distribution and Ecology

It is only to be expected that the available data on the distribution and, especially, the ecology of the South American Locust are very indefinite, owing to the unsatisfactory situation respecting its systematic position. Even if we assume that all the data to be found in the literature apply to one species, it is still an almost impossible task to outline the distribution of the species with any degree of certainty. The reason for this lies in the extremely unreliable information on the appearance of locusts in various countries of South America, where the usual practice is to mark as infested whole provinces where swarms have appeared. Thus, it becomes impossible to separate the areas through which swarms simply flew to places where the next oviposition took place from those where they bred. Even when the sites of oviposition are recorded, the data invariably refer to the years of mass outbreaks, and thus only the area of the largest distribution of the species can be determined, but not its permanent breeding area, which must be much more restricted.

The area covered during outbreaks can be, very roughly, determined as occupying nearly the whole of Argentina north of the 40th parallel, large portions of Uruguay, Paraguay, and Bolivia, and the western parts of Brazil; further north its swarms appear in Venezuela, migrating to Trinidad and some other West Indian islands, and through Colombia, Costa Rica, and Guatemala reach Mexico, though they usually invade only the southern parts of that country.

Numerous attempts have been made by local entomologists and anti-locust organisations to find out the permanent breeding areas of the locust, but with very little success. These failures are due to some fundamental mistakes on which these investigations have been based. To begin with, the idea of permanent breeding areas has been confused with the idea of areas for hibernation owing to the swarms of the locusts passing the winter in the imaginal diapause (see p. 267). Since hibernating swarms do not breed, the areas chosen for hibernation can hardly be expected to represent the actual areas of permanent breeding.

Another mistake has been due to the fact that investigators have always tried to find areas where locusts permanently breed in swarms. Though the phase theory cannot yet be fully applied to the locust in question, it stands to reason that no species of locusts can be expected to breed in swarms permanently, and in periods of minimum it must appear as a solitary grasshopper, even if there is no distinct solitary phase. In other words, the areas of permanent breeding are those where the species survives the minimum periods in a solitary state. Though no one has ever attempted to find areas of this kind, I firmly believe that they exist and that they are much more restricted than the areas which are subject to invasions during outbreaks.

Investigations of permanent areas are possible only on an ecological basis, but so far our knowledge of the ecological requirements of this locust is absolutely nil. There are, of course, a certain amount of data on the character of the places selected for oviposition by invading swarms, but we know that data of this kind do not reveal the normal habits of any species. Hoffmann (1925) is inclined to regard the American locust as an insect of a damp tropical habitat, but this is hardly in agreement with its distribution in the more southern parts of Argentina, where it seems to be connected with dry open grassland.

One point that may be regarded as of value for future research is the obvious inclination of migrating swarms to lay their eggs in cultivated places, that is in more or less soft and damp soils. This seems to point to the fact that the normal breeding habits of the species may also be connected with habitats of a similar kind, perhaps with river valleys, but it would be useless to speculate on this problem, which requires detailed investigations on the spot.

Bionomics

There is still much that is not clear in the bionomics of the South American locust, and much of the data is contradictory. The best connected accounts on the life history have been given by Bruner (1898) for Argentina and by Dampf (1925) for Mexico.

In Argentina the eggs are laid by invading swarms in spring (September to November). The number of egg-pods laid by one female is stated by some authors to reach as many as seven or eight, but no definite evidence is known to me in support of this statement. Hatching occurs after 25–60 days, and the larval development takes, on the average, 50 days.

This summer generation of locusts, according to various authors, is unable to reproduce itself immediately after reaching the adult stage, and a very prolonged imaginal diapause (see p. 50) is necessary before the sexual products begin to develop. The swarms consisting of new adults at first make only small circular flights, but gradually these assume more serious proportions, and result in a series of more direct flights that are supposed to lead them to the region where the locust has to hibernate. Numerous maps and more or less ingenious schemes of movements of the spring invading swarms and of those of the summer generation exist, but they are none of them very convincing. Bruner (1898) suggests that the invading swarms proceed from their winter quarters, probably in the Chaco, towards the more settled districts, while the summer swarms, *i.e.* their progeny, move in the opposite direction, and finally reach the same winter quarters. Statements of this kind can be substantiated only by very numerous observations on definite swarms, not on records of the appearance of swarms of locusts in different districts, since under these circumstances it is easy to mistake disconnected movements of various swarms for the regular progress of a single one ; so far, no attempts have been made to study the movements of separate swarms during a sufficiently long period, and this could be done, perhaps, only by the aid of aeroplanes.

The idea of special winter refuges of the locust where its swarms remain in a sexually immature state until the next spring, is firmly established in South America, and several attempts have been made to locate these mysterious areas. One of these expeditions in 1917 (Lizer, 1919) deduced from the evidence collected from local inhabitants that a very important hibernating area is situated on the borders of Argentina, Paraguay, and Bolivia along the valley of the river Pilcomayao ; to this area swarms of locusts congregate from all directions in the autumn, and from it they disperse, also in all directions of the compass, in spring. It was a remarkable proof of a great desire to find at any cost a " permanent area of hibernation " that the expedition arrived at the above conclusion without finding any locusts in the region traversed ; the extremely contradictory evidence of the natives was considered sufficient to elaborate even the exact boundaries of the area.

In view of this obvious failure of the expedition to clear up the mystery of winter refuges, Lahille (1920) expressed a well-founded criticism of the whole theory of special hibernation areas, and suggested that the summer swarms do not migrate for hibernation anywhere ; in support of this view, which appears to me perfectly correct, he records numerous cases of swarms being observed in the central parts of Argentina during the winter months. Thus, the swarms composed of sexually immature individuals might simply make irregular flights throughout the winter, if the weather is warm ; on cold days the locusts, apparently, collect on and under bushes, and it is only towards spring that their movements begin to assume more regular features and become more prolonged ; in other words, we can observe here the phenomenon, usual in all true locusts, of a migration flight due to the approach of sexual maturity (see p. 86). It is not impossible that Lahille's theory must be further supplemented by the admission that the swarming habits of the locust in sexually immature swarms are reduced and that the swarms in autumn and winter tend to disperse, only to segregate again in spring, when higher temperatures and the approach of sexual maturity should favour gregarious habits ; the same suggestion has been made with regard to *S. gregaria* (see p. 255). If it is so, then even the absence of records of hibernating locusts in the areas near cultivation becomes easily explained ; no one would dream of reporting isolated locusts, or even small swarms, while it appears that even the local entomologists have never interested themselves in the winter Acridid fauna of the country, in the firm belief that the locust occurs only in swarms.

Thus, the normal annual cycle of the American locust seems to be as follows : oviposition in spring ; hatching without an embryonic diapause ; development of hoppers ; transformation into the adult stage about the end of the summer ; a very prolonged period of somewhat inactive life of sexually immature adults ; beginning of maturity, manifested externally by a change in coloration (see above) ; migration and oviposition. It is remarkable that the same annual cycle as in Argentina, with its fairly cold winter, is observed in Mexico, where the imaginal diapause cannot be ascribed to climatic conditions in winter that are unfavourable to sexual development (Dampf, 1925) ;

apparently, a firmly established rhythm in development is responsible for this fact.

Bruner (1898) suggested that sometimes a double brood in a year is not impossible, since there are records of oviposition during the end of summer. While more definite reports are lacking, there is no definite reason to doubt the possibility of a second generation in exceptional cases and, above all, when the locust invasion is coming to its natural end by reversion to the solitary phase, which, by analogy with other species, may be able to develop without either embryonic or imaginal diapause. This is, of course, only a theoretical suggestion, and it must be tested by careful observations.

With regard to behaviour, the American locust does not seem to differ from other locusts, though it is worth mentioning that no observations of any value have been made on the subject, picturesque descriptions of mass movements of larval bands and swarms constituting all the information.

The feeding habits of the American locust have also never been properly studied. Bruner (1898) is inclined to regard the locust as very unrestricted in its choice of food plants, but unfortunately he does not state whether his observations refer to the hoppers or to the adult swarms. From some of his statements, it seems that the greatest damage is done by adults of invading swarms, which attack even trees ; we know that this may happen not from hunger, but from thirst (see p. 74). He states that grasses and cultivated Graminaceous plants are amongst the preferred food plants, but that *Sorghum* and allied plants are seldom injured and then only by the adults. No Cucurbitaceæ, wild or cultivated, or milk-weeds (Euphorbiaceæ) are eaten. From other parts of South and Central America and the West Indies, there are records of damage to a long list of various cultivated plants, but again mainly by invading swarms, while information on the normal food of the hoppers is practically lacking.

Periodicity

It is practically impossible to arrive at any idea as to the extent of fluctuations in the numbers of locusts in South America, since official reports indicate their presence almost every year, while there are no figures apart from the acreage of " invaded " areas which are meaningless. Nevertheless, certain years show a marked increase in devastations, and this may be taken as evidence that the numbers of locusts in South America fluctuate as they do in other countries.

So far the problem of periodicity of the South American locust has remained absolutely unstudied. Nothing is known about this locust during the years of minimum, when everybody seems simply to forget it until the next outbreak. It is only very recently that Dampf started some investigations in Mexico on this problem, and he immediately arrived at some extremely interesting conclusions. His observations and experiments (1925, 1926) show that in *S. paranensis* the same phenomena of transformation of typical swarming black and yellow-coloured hoppers into uniformly green ones can be observed in connection with crowding, or dispersal of bands (Fig. 91, 3 and 4). He

suggested that there is in this species, as in others, a solitary phase, and it is represented by *S. americana*. The presence of hoppers coloured differently from the typical swarming ones, in the bands of the latter (probably in the period near the end of an outbreak), has been noticed by some other writers, and Marelli (1916) published detailed descriptions of such aberrant hoppers, and of the adults bred from them. This author was inclined to think on the strength of his observations that the number of species of *Schistocerca*, as usually accepted, must be greatly reduced, since many of them are probably only colour forms. His observations and, particularly, those of Dampf dispose of the suggestion made by Bruner (1898, 1900) that certain species of *Schistocerca*, almost indistinguishable in the adult stage, can be very easily separated by the coloration of the hoppers; it is clear now that the coloration of the hoppers in *S. paranensis* is not specific, but extremely easily influenced by the conditions of breeding—in dense aggregations, or singly.

When *S. paranensis*, as a swarming form, is compared with *S. americana*, which does not swarm, the differences between them are very much smaller than between, for instance, *Locusta migratoria* and *danica* (see p. 148). It is, therefore, extremely probable that Dampf's view regarding two "species" of *Schistocerca* is correct, while several other "species" may be also involved.

Only careful field studies during the years of minimum of locusts and well-organised laboratory experiments can throw light on the problem of periodicity of the South American Locust, and the sooner such work is started the better from a practical point of view.

The Locust Problem in South and Central America

One very curious feature of the locust problem in South America is its practical permanency. The following table of official figures offers a good illustration of this point (Institut Intern. Agric., 1916, 1926):

	Invaded territory in sq. km.		Invaded territory in sq. km.		Invaded territory in sq. km.
1897–98	1,400,000	1907–08	1,307,000	1917–18	822,406
1898–99	810,000	1908–09	1,320,000	1918–19	810,130
1899–00	553,000	1909–10	1,350,000	1919–20	720,000
1900–01	80,000	1910–11	891,000	1920–21	800,000
1901–02	68,000	1911–12	204,152	1921–22	1,148,131
1902–03	120,000	1912–13	14,871	1922–23	1,419,760
1903–04	500,000	1913–14	758,517	1923–24	1,152,730
1904–05	600,000	1914–15	1,000,000	1924–25	1,228,283
1905–06	873,000	1915–16	1,287,681		
1906–07	1,140,000	1916–17	1,316,225		

There is, probably, no other country in the world (apart from other South American Republics) where locusts are a *permanent* pest, invading in some years as much as 48 per cent. of the whole territory of the country, as happened in Argentina in 1922–23. While there can be no doubt that the figures are grossly exaggerated and under "invaded" areas must be understood whole districts in which the presence of locusts was reported, still it is remarkable that during a period covering nearly thirty years there was not a single year free from locusts, the more so that 1899 must be considered in Argentina as the year when regular control of locusts was inaugurated by the establishment

of the " Defensa Agricola." Each year enormous sums of money are expended on the anti-locust measures, and millions of kilograms of the insects are reported destroyed, but the figures of the extent of locust invasions from year to year demonstrate most clearly that the work has no practical effect on the course of events. There can only be one explanation of these remarkable facts, namely, that the organisation of control is ineffective. Let us see what the organisation is.

By the law of 1898, all inhabitants of the Republic, from 15 to 50 years old, are obliged to fight locusts, for a nominal remuneration, anywhere within ten kilometres of their homes, the total number of working days during a season not to exceed twenty; it is permitted to hire other persons to do the work, or to pay a tax instead, or else to present a fixed amount of killed locusts or their eggs. The Government distributes, gratis, materials necessary for the work (flame-throwers and naphtha, barriers, etc.), collects information on the movements of swarms, and issues warnings to threatened districts. At the head of the organisation, there is a central commission of the " Defensa Agricola," consisting of six members, while during the campaigns, district inspectors are appointed, whose duty it is to see that the work is carried out.

Even if it is admitted that the reasons which were given in Chapter IX of the present book are not sufficient for bringing to an end the system of control based on compulsory labour, the whole history of its practical application in Argentina and other South American republics is a deadly condemnation of that system. It may be argued that the area of enormous uncultivated lands in that country makes it impossible to apply another system, not merely defensive (and that in a doubtful degree), but directly offensive against locusts. I maintain, however, that wholly satisfactory results could be obtained at the same expense (counting the labour, which is not fully paid), but with an organisation based on different principles, namely, headed by responsible specialists and conducted by paid labour and more efficient methods. As regards the latter, the barriers so widely and skilfully applied in South America must be considered very effective, but only the introduction of poisoned baits would permit of an attack on the locusts, and not merely defend the crops from them. Baits and chemical methods generally meet in South America with stubborn and wholly unfounded objections on the part of the administration and the landowners on account of the possible danger to domestic animals. In other countries, however, where cattle breeding is just as important as in South America (South Africa, Russia), arsenicals are employed against locusts on a very large scale, and no disastrous results are known.

The technical side is, however, much less important than the organisation, since even with the introduction of the best possible methods the present system can give rise to no better results than it produces at present.

Another extremely important point about the locust problem in South and Central America is the lack of knowledge on the most essential questions of the locust bionomics, distribution, etc. Attempts to establish some research institutions have not been lacking in the past, but somehow the results

obtained are practically nil ; the only exception is offered by the work which is being at present carried out in Mexico by Dr. A. Dampf in a special laboratory ; similar work, on a much larger scale, is absolutely necessary in other South American countries, if there is a sincere wish to settle the locust problem.

There are, of course, other special difficulties in the way of the solution of the locust problem in South America. One of them arises from the fact that the territories subject to locust invasions belong to several States, and this leads to continual controversies, as to whose " swarms " are responsible for invasions. A special formal agreement was entered into between Argentina, Bolivia, Brazil, Paraguay, and Uruguay as long ago as 1913, but it provided only for an exchange of information on the movements of locust swarms and contained a formal obligation on the part of each State to control locusts on its territory. Again, the facts of uninterrupted locust invasions demonstrate with sufficient clearness that the efficient control of the plague cannot be attained by any international conventions or legislation. It is, perhaps, too much to hope at present that an international organisation for actual control could be established in South America, but at least effective organisations in each country and an international organisation for research are amongst the urgent needs.

Another difficulty is due to the peculiar life-cycle of this locust, owing to which only a relatively short period separates oviposition from the hatching of the hoppers. This makes it practically impossible to make a proper survey of infested (not merely invaded) areas and to prepare for the campaign against the hoppers at leisure. It seems, therefore, that preparations for the campaign must be concentrated during the winter period, before the invasion begins. At the same time, it ought to be perfectly possible to organise an effective service for the extermination of hibernating swarms, even if they actually migrate to some special refuges, which is highly improbable. The present method seems to leave hibernating swarms in peace, since they do practically no damage, but this is obviously a very short-sighted policy. Indeed, the control of hibernating locusts, as being a source of future invasions, must be considered the most important part of a campaign, the measures against the hoppers coming next in importance, while attempts to destroy new swarms can only be futile.

On the whole the difficulties, though great, are not insurmountable, but they can only be overcome after a drastic reform in the present organisation, the mere enlargement of which will not help matters.

CHAPTER XIV

THE BROWN LOCUST (Locustana pardalina, Wlk.), THE RED LOCUST (Nomadacris septemfasciata, Serv.), AND THE LOCUST PROBLEM IN SOUTH AFRICA

Species of Locusts in South Africa

The chief destructive species of locust in South Africa is *Locustana pardalina*, Wlk.. which has also been recorded under its synonyms, *Pachytylus sulcicollis*, St., and *P. capensis*, Sauss. (Uvarov, 1921). There are, however, several other species that swarm periodically, or occasionally. These include the Red (or Red-winged) Locust of local reports, *Nomadacris septemfasciata*, Serv. (with its synonyms *Cyrtacanthacris fascifera*, Wlk., *C. purpurifera*, Wlk., *C. subsellata*, Wlk.). *Acridium coangustatum*, Luc., and *A. sanctae-mariae*, Fin., also belong here, but represent a special form of the species, which will be discussed later (see also Uvarov, 1923).

While the two locusts mentioned are the only ones recognised (but often confused) in official reports and more popular literature, there are scattered reports of other species appearing less regularly, or, perhaps, simply confused with one or the other of the two common species. Thus, the Desert Locust, *Schistocerca gregaria*, is a not uncommon insect, especially in South-West Africa, where it is known to occur both in the swarming and the solitary phase (Uvarov, 1923), but has never been recorded as swarming. This may be due to confusion with the Red Locust, as they have a considerable superficial resemblance.

Further, the Migratory Locust (*Locusta migratoria*, L.) is not only known to occur in the country, but occasional swarms were even recorded of its tropical phase (*migratorioides*) in 1924, particularly on the border of Rhodesia and Portuguese East Africa (Lounsbury, 1924). There is little doubt that this species has occurred in swarms on other occasions, but it is likely to be confused with the common Brown Locust and recorded as such. It is highly probable, also, that this species may give trouble in the future in parts of the country that are near the swamps of the Zambesi and others.

The large Tree Locust, *Anacridium moestum*, Serv., is a species that swarms occasionally (see p. 319), and damage from it has been recorded in the Orange Free State (Lounsbury, 1924), but local observers, familiar only with the two common species of locusts, would always confuse it with the Red Locust.

The Elegant Grasshopper (*Zonocerus elegans*, Thnbg.) is also a common pest in the country, but its gegarious habits are not regular, and we will return to it in another chapter (see p. 312).

Thus, it will be seen that there are in South Africa two species that are common and three more that appear occasionally in swarms, but are undoubtedly very often mistaken for the others ; moreover, even the two common species are not always recognisable in the official reports, and this often makes utilisation of them impossible.

In the present chapter I will describe only the two more common species, while data on the others must be looked for in respective chapters of the book (*Anacridium moestum*, p. 319 ; *Zonocerus elegans*, p. 312 ; *Locusta migratoria*, p. 237 ; *Schistocerca gregaria*, p. 250).

Description of Stages of the Brown Locust

Adult Insect of Swarming Phase (ph. *pardalina*, Wlk.) (Fig. 71). Antennæ somewhat flattened. Frontal ridge widened at the median ocellus. Pronotum feebly compressed from the sides, but strongly constricted before the middle ; median keel raised, but distinctly lower in the front half than in the hind ; transverse furrows deep, the hind one placed before the middle of the pronotum ; front margin straight ; hind angle rounded. Elytra extending beyond the hind knees, rather broad, with the apex obliquely truncate, false vein in the discoidal area thick and sinuate (Fig. 71, C). Hind femora broad. Male cerci rather large, compressed laterally. Males only a little smaller than females. Coloration yellowish-grey (or sulphur-yellow in sexually mature individuals) ; elytra in the apical half transparent, with an oblique series of small brownish spots ; hind femora with ill-defined dark bands above ; hind tibiæ yellowish, with the spines black. Length, male 41–45 mm., female 42–46 mm. ; elytra, male 42–46 mm., female 44–48 mm.

Adult of the Solitary Phase (ph. *solitaria*, Uv.) (Fig. 71).—Smaller than the swarming phase ; males much smaller than females. Pronotum more compressed laterally between the shoulders, but less constricted before the middle ; median keel more raised, not lower in the front portion than in the hind ; front margin projecting in the middle ; hind angle acute. Elytra shorter and narrower, false vein of the discoidal area not incrassate and straight (Fig. 71, F). Coloration very variable, often green and mottled with brown and black ; pronotum very often bears a whitish X-shaped design. Length, male 26–31 mm., female 30–36 mm. ; elytra, male 26–29 mm., female 36–42 mm.

Hopper of the Swarming Phase, First Stage (see coloured figures of hoppers and adults in Faure, 1923 ; descriptions also in Sander 1902).—At first yellowish in colour, but the ultimate coloration is black, without any pattern (no morphological description of this or other stages exists).

Hopper of the Swarming Phase, Second Stage.—Mainly yellow, with sharp black markings ; median keel of pronotum and large spots, one on each of its sides, are black ; abdomen with blackish and yellowish stripes. Length about 10 mm.

Hopper of the Swarming Phase, Third Stage. — General coloration becomes reddish-yellow (on which the local name for hoppers, *rooibaatjie*, is founded) ; black markings of the same general shape ; on the hind femora

appear traces of dark bands. Rudiments of elytra and wings still directed obliquely downwards, black. Length 15–18 mm.

Hopper of the Swarming Phase, Fourth Stage.—The orange colour becomes deeper, black parts reduced in size, but very conspicuous. Rudiments of elytra and wings turned up, black. Length 20–22 mm.

Hopper of the Swarming Phase, Fifth Stage.—The same general scheme of colours remains; black areas more reduced, but sharp. Rudiments of elytra and wings large, black. Length 24–28 mm.

Hoppers of the Solitary Phase.—Extremely variable in colour, often green, brown, grey, even black, mostly with a whitish X-shaped design on pronotum.

Egg-pod. Varying in shape, mostly cylindrical, somewhat bent. Upper half, or one-third, consisting of a soft, spongy mass, forming the stopper. Walls soft and fragile. Eggs up to 82 in number, arranged in rows.

Distribution and Ecology of the Brown Locust

It is very difficult to define the area of distribution of the Brown Locust, even in the years of mass outbreaks, with sufficient exactitude, since old records, apparently, recognised no distinction between the species of locusts; still more difficult is it to define the area of distribution of the solitary phase or the ecological requirements of both phases.

A study of the maps of various invasions (see South African Central Locust Bureau, Reports I–IV, also annual reports of the Department of Agriculture of South Africa) shows that in no case has the whole of South Africa been invaded by the Brown Locust, and certain parts of it appear to be altogether exempt from its visitations. According to Lounsbury (1915), it is pre-eminently an inland species, and its swarms, while invading the interior of the country, reach the coastal districts only between Algoa Bay and the mouth of the Key River. Thus, the south-western limit of more regular invasions seems to be formed by the barren western Karroo. To the south-east, Natal is only visited in exceptional cases by swarms of this species, and here the Red Locust entirely replaces it. The northern limits of distribution, or of migrations, are not very clear, but in Southern Rhodesia swarms of the Brown Locust sometimes reach the northern boundary of the country, and the same applies to the South-West African Protectorate and Bechuanaland.

As is usually the case with such a strongly migratory species, the distribution of the Brown Locust during the years of outbreaks has only a remote relation to its distribution in the periods of minimum, *i.e.* when in the solitary phase. Faure (1923) has given some very brief data on the distribution and ecology of the solitary phase; according to him, it is restricted to the Karroo, the north-western parts of the Cape province, the western portion of the Orange Free State and adjoining areas, where "the short mixed veld, consisting of grass and Karroo bush and sandy soil with limestone outcrops, gives the locust what appear to be its favourite natural breeding grounds; the best spots to look for these solitary individuals are the hard limestone patches in red sand country."

If the area so defined is compared with the botanical map of Africa (Shantz and Marbut, "The Vegetation and Soils of Africa," American Geographical Society : Research series, No. 13 ; New York, 1923), it appears that the home of the Brown Locust coincides with the Desert grass—Desert shrub formation ; since the area occupied by the latter extends in the shape of a narrow belt far northwards into the South-West African Protectorate (and even into Angola), we may expect that the normal breeding grounds of the Brown Locust ought to exist there as well ; indeed, the maps of distribution of swarms indicate that this is actually the case.

Of course, these considerations as to the location and ecology of breeding grounds of the Brown Locust must be regarded as purely preliminary and merely forming a starting-point for future investigations, but they mark a distinct progress in the right direction, if compared with older views, when the whole blame for invasions of cultivated districts was laid to the Kalahari desert, in the remote interior of which mysterious permanent breeding areas were supposed to exist. The Kalahari undoubtedly plays a very important part in the course of invasions, acting as a very favourable temporary region, but this aspect of the problem will be discussed later.

From the maps of various invasions there emerges one curious fact : their extent in a northward direction may be enormous—up to the northern limits of Rhodesia—but, as has been said above, swarms scarcely ever penetrate in a south-western direction beyond the most arid Western Karroo. What the reason for this is, is difficult to say ; the uplands of the Karroo are certainly not high enough to be a physical obstacle to flying swarms, while their extent is too small to prevent swarms crossing them and descending into more fertile districts nearer the coast. It seems fairly certain that swarms migrating from their breeding grounds are prevented from moving westwards by prevailing winds ; this is only a suggestion which must be verified by studies of wind records for the respective periods.

There are no ecological data on the places selected for actual oviposition by the solitary phase, or even by the migrating swarms.

The Life History of the Brown Locust

It is a very regrettable fact that the existing information on the bionomics of the Brown Locust is only fragmentary. To begin with, the annual life cycle cannot be considered definitely known. While Fuller (S.A. Central Locust Bureau, Second Report, p. 2) states definitely that the Brown Locust must be regarded as single brooded and points out the absence of direct evidence of a second brood, Lounsbury (1915) believes that there are two broods in a year, one case of two successive generations in a year having come under direct observation in an isolated outbreak in midland districts of the Cape Province. According to Lounsbury, the invading swarms appear in March, or later, and deposit their eggs before winter ; they hatch after the first soaking rains of the warm season, generally in October, and the adult stage is reached in about two months. Thus the time of hatching depends entirely on the rains, and, consequently the hatching period may extend over a very long time if the egg

deposits are scattered in districts with varying rainfall, and this may to a great extent be responsible for the differences in time of appearance of the flying swarms ; indeed, Fuller (*l.c.*) believed this to be the reason for the very late appearance of swarms, which may be mistaken for swarms of a second generation. Lounsbury, however, insists that this is not so and that swarms of the first generation lay their eggs about a month after the adult stage is reached, and the hatching may occur within another month.

Both views are based on indirect evidence (apart from the one case quoted by Lounsbury), and both may be right, since there is every reason to suggest that the annual cycle of the swarming phase may be different from that of the solitary one, while in the transitory periods a considerable confusion in the cycle must be expected. It appears probable that the solitary phase may produce several generations a year, and the swarming phase one only, with a long diapause in the egg stage. In any case, there is no reason to suggest a long imaginal diapause, such as occurs in the Red Locust (see below).

Another doubtful point of considerable practical interest is the number of egg-pods laid by one female. Faure (1923) obtained up to 14 pods from three females kept in cages, while the average number laid under these conditions, which he rightly calls " very abnormal," was about five pods per female. It would be very unsafe to conclude from these data that similar phenomena occur under natural conditions, since it is well known that female ACRIDIDÆ in cages live much longer than in the field and can lay eggs almost indefinitely. Direct observations in the field are, of course, lacking, or unreliable, and refer to whole swarms, not to single individuals. An answer to the question might perhaps be obtained by keeping isolated females in large insectaries under conditions as nearly natural as possible.

The shortest incubation period observed by Faure in cages was 15 days, but the eggs laid late in the season hibernate and hatch only after first rains in spring. His statement, that " eggs laid during the summer hatch after the first rain, whether this falls a week or three months afterwards," does not seem to be based on direct observations, in any case, not under experimental conditions, so that the problem of the length of embryonic diapause in the Brown Locust remains unsolved. One aspect of the problem is, however, clear, and that is the extraordinarily long diapause of the eggs kept under dry conditions ; Lounsbury (1915) obtained hoppers from eggs kept dry for $3\frac{1}{2}$ years, but, unfortunately, no observations were made on the stage of embryo during which the eggs were dormant. For a general study of the embryonic diapause in eggs of ACRIDIDÆ, the Brown Locust must be an excellent subject.

Apart from some purely popular descriptions of movements of bands of hoppers and flying swarms, there is no information available on the behaviour of the Brown Locust and the factors regulating it ; investigations in this direction are obviously wanted as they may be of direct help in control.

PERIODICITY OF THE BROWN LOCUST

Periodic fluctuations in the numbers of this locust are well known, but their cause is still very far from being clear. Lounsbury (1915) was inclined to seek

an explanation of its periodicity in climatic fluctuations ; and one of the chief causes of a sudden increase in numbers of the locust after a prolonged drought is, in his opinion, the ability of the eggs to preserve their vitality without hatching for several years ; this may enable eggs to accumulate during a series of dry years and then all hatch together under the influence of a good rainy season. This reasoning is largely theoretical and not free from difficulties. If locusts are very scarce over a series of years, there cannot be a very large accumulation of eggs even for several years ; moreover, the longer the eggs remain in the ground, the more they are exposed to attacks from their natural enemies (Bombyliids, Mylabrids, etc.) ; this latter point has, apparently, been overlooked hitherto.

The work of Faure has shown clearly that at least a partial solution of the problem of periodicity in the Brown Locust must be looked for in its ability to transform from one phase to another (see Chapter VII, p. 155), and further research on its periodicity cannot be successful if this point of view is neglected.

Description of Stages of the Red Locust

Adult of the Swarming Phase (ph. *septemfasciata*) (Fig. 92, S, E). Face vertical ; frontal ridge not dilated at the ocellum. Pronotum somewhat sellate, constricted before the middle, rounded ; surface of pronotum rugulose ; median keel scarcely perceptible ; no trace of lateral keels. Prosternum (between the bases of front legs) with a strong spine bent backwards. Elytra very long ; reticulation in their basal half finer and denser than in any other species of this size, the cellules between the veinlets being minute and elongated (Fig. 92, R). Coloration brown or reddish-brown, often with a pale dorsal stripe, with blackish pattern. Elytra with several oblique parallel brownish fasciæ. Wings hyaline, or pink at the base (this latter colour, probably, present only in sexually immature individuals). Hind tibiæ red. Length, male 51–56 mm., female 60–65 mm. ; elytra, male 49–57 mm., female 56–64 mm.

Adult of the Solitary Phase (ph. *coangustata*, Luc.) (Fig. 92, C).—Differs from the preceding only by its longer pronotum, which is also not constricted in the middle, but simply narrowed forward. Coloration and measurements the same.

Hoppers.—No descriptions of the hoppers exist. The figure given in the Fourth Report of the South African Locust Bureau shows a hopper of the last stage, which is reddish-brown in colour, with a dark (black ?) dorsal stripe.

Egg-pods.—There is no description of the egg-pods, but judging from the figure in the Fourth Report of the Locust Bureau, the eggs are laid in a rather loose cluster, without or with but a very thin and fragile outer cover.

Distribution and Ecology of the Red Locust

Our knowledge of the distribution of this species is very scanty. It appears to occur throughout the whole of South Africa, while northwards its area extends to the lower course of the Congo River in the west and to the Southern Sudan and Abyssinia in the east. The species is known also, but only in the solitary

phase (*coangustata*), from Madagascar, Réunion, and the Comoro islands ; this phase is also definitely known from Uganda, the Congo, Rhodesia, and the Transvaal (Uvarov, 1923). Within this area, the Red Locust is known to swarm mainly in the coastal belt of Natal and Portuguese East Africa, and the swarms then spread far into the Transvaal, Cape Province, Orange Free State, and Rhodesia. It would seem that the conditions for swarming of this species are a very high humidity and generally a climate of a tropical type, but nothing is known as to the actual conditions of its breeding.

The Life History of the Red Locust

Information on this point is again extremely meagre. Lounsbury believes that this locust produces only one generation a year, the adults passing the

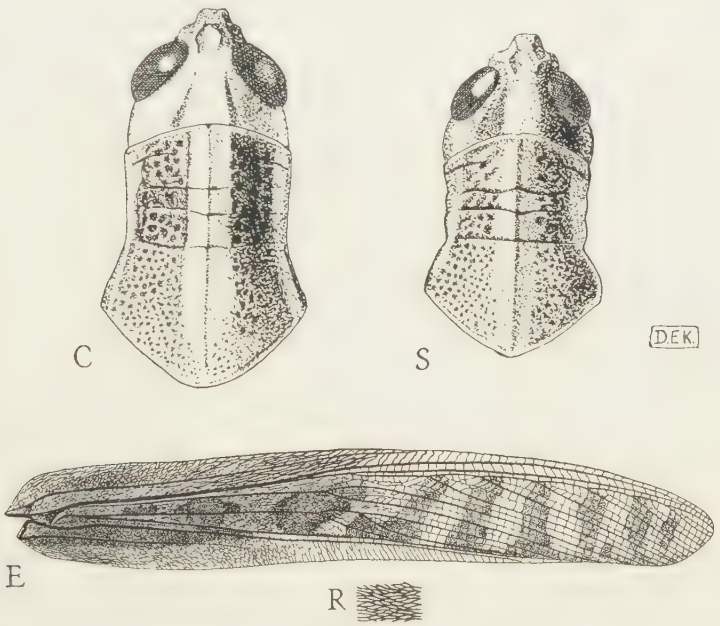

Fig. 92.—Red Locust.—S, swarming phase.—C, supposed solitary phase (*coangustata*).—E, elytron.—R, portion of the base of elytron greatly enlarged to show the fine reticulation (original).

winter (presumably in forests) in a sexually immature state. They pair in spring, and the migrations of swarms also occur at this season. Oviposition was observed in Natal early in October, but early December is considered the normal time in that province. The incubation period is estimated by different authors at about thirty days, and hatching is said to occur without such strict dependence on rains as in the case of the Brown Locust. The development of the hoppers occupies about two months (Howard, 1910).

Thus in the Red Locust we meet with the same type of annual cycle as in species of the genus *Schistocerca*—one annual generation and a very long imaginal diapause during winter.

Nothing is known of the life cycle or bionomics of the solitary phase.

The Locust Problem in South Africa

From the point of view of national economics, the locust problem in South Africa is, perhaps, of greater importance than anywhere else, while its history reaches back to the times even before the settlement of Cape Town. Since the very first years of European settlement and until the present day, the country pays to locusts a tremendous annual tribute, only fluctuating in its size, but hardly ever absent. It is only natural that great attention has been paid to the proper organisation of control with results that are considered very satisfactory, though to an outside observer they appear to justify some analysis.

South Africa was the first country to introduce spraying with arsenical poison, and this method has since spread over the whole world. A permanent anti-locust organisation also appeared in South Africa long before anywhere else, and at present it is organised on a scale far exceeding similar organisations of other countries, while most of the latter have no organisation at all. In view of all this, it would seem somewhat surprising that the locust question in South Africa is still one of the greatest national problems. It would appear that the control measures are mainly effective in the direct defence of crops from destruction, and that little progress is being made towards the prevention of outbreaks, or, at least, shortening their incidence. The reason for this seems to be in the general principles of organisation for locust control, which is based entirely on the law forcing all occupiers of land to exterminate eggs or hoppers before they reach the adult stage, the choice of methods being free, though arsenical poisoning is recommended and the Government supplies sprayers and poison free of charge. Specially appointed locust officers instruct farmers in the use of poison and also compel them, when necessary, to take measures against locusts. It is hardly necessary to discuss here all the disadvantages of this system, since they have been fully described on pp. 204–208, and it is reasonable to suggest that great improvements in general results might be attained by a gradual transition to the system of fully paid labour. There would be no new departure in introducing this principle in South Africa, since at present the work on unoccupied lands is done by paid labour under locust officers, and it only remains to extend the system to all lands. Under this system, farmers would be relieved of the necessity for giving their labour free even when they are not immediately interested in locust control, as is the case with stock-raisers. There is little doubt that a special tax for locust control would be more welcome to the farmers than the present system, which is both unfair to those in infested districts and not wholly effective, without being very cheap.

Only such a system, as outlined, would enable the locust administration to organise a really effective control of locusts everywhere as well as during the years of relatively small outbreaks, when only small and scattered swarms of locusts appear; such swarms, it may be supposed, remain often now unreported and are not destroyed, only to give rise to larger swarms. The farmers, when they no longer have to fear the trouble and necessity of working on locust destruction, will gladly report even the smallest swarms, and these can be easily

and cheaply exterminated; outbreaks may thus be prevented from developing to serious dimensions.

Another feature of the locust problem in South Africa is our remarkably limited knowledge of the locusts concerned and the most essential details of their bionomics. The necessity for research on locusts is realised, no doubt, but so far practically nothing has been done in that direction, though a special research laboratory has recently been established. There can be no doubt that correctly directed and well-organised research must produce results of immediate practical importance, and not of scientific value only, as has sometimes been suggested (Lounsbury, 1924). Thus, the problem of breeding areas of the Brown Locust must help in organising a proper control of this locust before its outbreaks develop to such an extent as they have been permitted to do in the past. Further, a study of the ecological conditions of these areas may suggest some means of dealing with them in a way unfavourable to the swarming phase of the locust, etc.

CHAPTER XV

THE ITALIAN LOCUST (Calliptamus italicus, L.)

Before describing the stages of development of the Italian Locust, I must point out that our knowledge of the systematic status of this pest is very unsatisfactory. *Calliptamus italicus*, L., is usually described by systematists as highly variable in size, proportion of body, coloration, etc., but these variations are always considered individual and of no practical interest. There is no doubt that this view is erroneous, and that under the name *C. italicus* are confused several good species, some of them, perhaps, presenting more than one constant form which differ from each other not only morphologically, but in their bionomics. It is not impossible also that some of the species are able to produce phases, but it is difficult to start on a study of this problem until the systematics of the genus has been cleared up and the diagnostic characters of the species established. The progress of our knowledge of this pest is thus at a standstill.*

Description of Stages

Adult Insect (Fig. 93).—Coloration very variable, from dark-brown to pale greyish or yellowish-brown, unicolorous or more often with numerous grey or brownish small spots ; a common colour variation consists in the presence of white stripes along the margins of the pronotum. Pronotum above flat, with a low straight median keel and two straight lateral keels which slightly diverge backwards. Prosternum, between the bases of the front legs, with a straight blunt spine. Elytra usually reach the end of abdomen or exceed it (in some forms, or species, shorter than abdomen), with small brownish spots. Wings transparent, pink in the basal part. Hind femora thick, with three ill-defined dark bands ; on the inside red. Hind tibiæ red. The male differs from the female by its much smaller size ; male cerci very large, compressed laterally, and provided at the apex with two small black teeth. Length, male 16–25 mm., female 21–25 mm. ; elytra, male 12–21 mm., female 18–36 mm.

Hopper of the First Stage (Fig. 93, a, A).—Brownish-black, or black, with the following parts whitish or white : palpi, a spot on the hind angle of lateral pronotal lobe, hind margins of tergites, the whole underside of body, front and middle legs, the base and two bands of hind femora and a ring at the base of hind tibiæ. Pronotum without lateral keels. No rudiments of elytra or

* I am able to state here that a revision of the genus *Calliptamus* is at present being undertaken by Dr. W. Ramme, in Berlin.

wings. Antennæ 13-jointed, their tips pale. Length 5–6 mm.; hind femur 2·5–3 mm.

Hopper of the Second Stage.—Coloration variable. In some individuals the coloration of the first stage is preserved, or the pale parts increase, or the whole coloration becomes very pale, without definite pattern; on the lateral pronotal lobe there is often a dark spot surrounded with pale colour. Lateral pronotal keels distinct. Rudiments of wings and elytra distinct, directed downwards, with traces of veins. Prosternum with a conical tubercle. Antennæ of the male 16-jointed, of female 17-jointed. Length 6–7 mm.; hind femur 3·8–5·5 mm.

Hopper of the Third Stage (Fig. 93, b).—Coloration in this stage and in the later stages is variable and similar to that of the adults; hind femora always

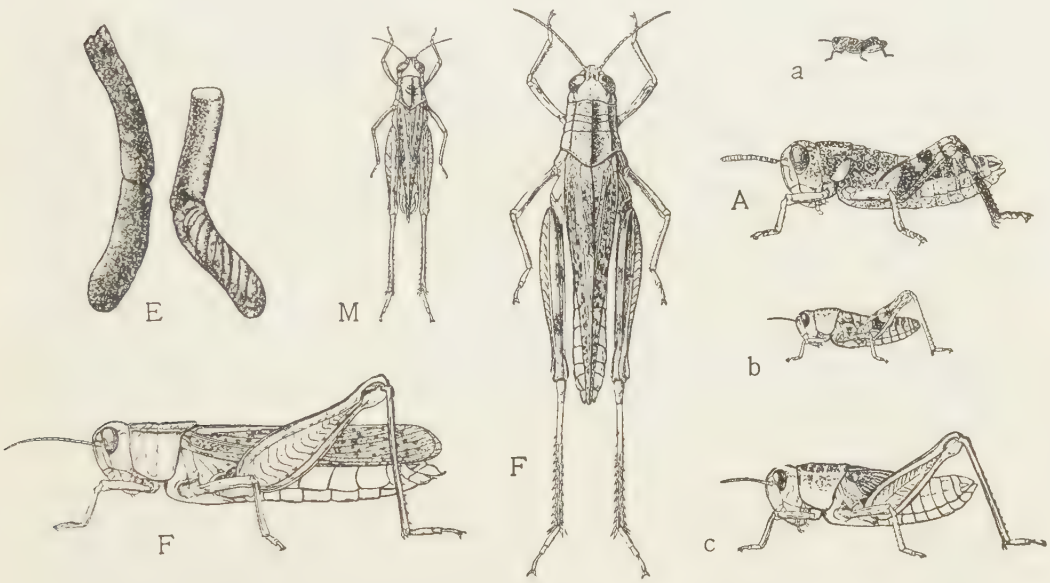

Fig. 93.—Italian Locust.—E, egg-pods.—M, male.—F, females.—a, hopper of the first stage.—A, ditto enlarged.—b, hopper of the third stage.—c, ditto of the fifth stage (after Plotnikov).

with two pairs of dark spots, and lateral pronotal lobe with a dark spot surrounded by pale colour. Prosternal tubercle long, pointed. Antennæ of the male 18–20-jointed, of the female 20–22-jointed. Length, male 11–13 mm., female 12–16 mm.; hind femur, male 5–6·5 mm., female 6–8 mm.

Hopper of the Fourth Stage.—Rudiments of elytra and wings turned upwards. Prosternal spine long, conical. Antennæ of the male 21–22-jointed, of the female 22–23-jointed. Length, male 10–14 mm., female 19–22 mm.; hind femur, male 7–9 mm., female 8–12 mm.

Hopper of the Fifth Stage (Fig. 93, c).—Wing rudiments reaching third or fourth segment of the abdomen, dark in colour. Prosternal spine and genital appendages almost as in the adult. Antennæ 23–24-jointed. Length, male 12–23 mm., female 21–24 mm.; hind femur, male 9–12 mm., female 9–15 mm. (All descriptions from Dovnar-Zapolsky, 1925, with alterations.)

Hopper of the Female Sex, Sixth Stage.—According to Plotnikov (1926), females of this species have a supplementary larval stage differing, apparently, only in size ; length of hind femur 12–20 mm.

Distribution and Ecology

Owing to the uncertainty in identification of these insects, the information on distribution and ecology cannot be exact and reliable, and some data may refer to different species.

On the whole the area of distribution of the Italian locust (or, rather, of the genus *Calliptamus*) is very similar to that of the Moroccan Locust (see p. 224, and Fig. 83), but extends considerably in all directions compared with that species.

Beginning from the West, the Italian Locust has been recorded from Madeira and the Canaries. On the latter islands, it is said to occur together with a local species (*Calliptamus plebeius*, Wlk., = *vulcanius*, Kr.), but this record is doubtful. As regards Madeira, another undescribed species also occurs there. No damage by the locust has ever been recorded in Madeira or in the Canaries.

In North Africa the Italian Locust is supposed to be very widely distributed, reaching even beyond the southern limits of the desert (Senegal, Khartoum), but this is a mistake, based on the superficial resemblance to the Italian Locust of a related genus and species (*Acorypha*, or *Caloptenopsis glaucopsis*, Wlk.), which is very common in the savanna zone south of the Sahara (and in the plains of India). The true *Calliptamus* occurs only in Morocco, Algeria, Tunisia, Tripolitania, and Egypt, *i.e.* it reaches the Sahara desert and only partially penetrates into it, producing there peculiar large and long-winged forms (or species ?). In Morocco and Algeria the species sometimes occurs in masses and causes damage.

There is, apparently, a peculiar local species of *Calliptamus* (with short elytra and large head) in Spain and Portugal, where there are no records of damage.

North of the Mediterranean the area of distribution of *Calliptamus* comprises the whole of France, Switzerland, Southern and part of Central Germany, Austria, Hungary, Southern and Central Russia. In Asia the northern boundary of its distribution is not clear ; eastwards, *Calliptamus* (probably another species) reaches the Pacific Ocean. Its southern limits in Asia are also not well known, but the insect occurs commonly in the plains of Mesopotamia, in Southern Persia, and even on the southern slopes of the Himalayas.

Within this wide geographical area, *Calliptamus* is known as a pest only in North Africa (Algeria mainly), Italy, sometimes France, Hungary, Southern Russia (Ukraine), Southern Siberia, Turkestan, and Persia. In many cases, however, the records referring to this locust are confused with those of the Moroccan Locust, and it is often quite impossible to decide which species was actually involved.

Ecological information on *Calliptamus* in countries where it occurs as a pest is scanty, except for Russia, where its ecology has been studied recently

by several entomologists (Moritz, 1914; Dovnar-Zapolsky, 1925; Kiritchenko, 1926). In Italy and France the locust occurs in dry fields with scanty vegetation. In Russia it is known to occur as a solitary grasshopper, though sometimes very numerous, in a variety of habitats, ranging from grass steppes to semi-deserts, but recent research has proved that its proper habitat is sage-brush (*Artemisia austriaca*) steppe occupying a broad zone along the northern coasts of the Black Sea, stretching eastwards into Western Siberia, and reappearing in Turkestan nearer to the mountains of Central Asia. The connection of this locust with *Artemisia* is very intimate since this plant is the main food of young hoppers. Sage steppe, apart from occupying the large natural area outlined above, is a plant association that is apt to invade the more elevated and drier portions of the grass steppes if they are overgrazed; in this case grasses give way to sage, and such places are common along roads, near villages (communal grazing grounds), etc., and they become very suitable breeding places for *Calliptamus*. Thus, penetration of this locust into grass steppes is to a great extent due to careless management of grazing grounds.

A characteristic feature of the distribution of *Calliptamus* is its very wide area and the absence of definitely localised breeding places. Indeed, outbreaks of it do not often occur, but apparently they may happen almost anywhere, there being no localities liable to regular invasions.

Bionomics

The ecological conditions for oviposition are not very exactly known, but there is no doubt that *Calliptamus* usually lays its eggs not only in the virgin soil of the sage-brush steppes, but also in relatively loose soils, provided that they are dry and vegetation is not dense. Such conditions are often realised on lands ploughed two or three years previously in the immediate vicinity of crops, and this makes the species particularly dangerous to them.

The period of oviposition begins later than in the Moroccan Locust. The females during oviposition sometimes congregate in dense groups, with the result that the deposition may be very concentrated; Filipjev (1926) records cases when as many as 4000 egg-pods were counted to a square metre.

Hatching usually occurs very unevenly, extending sometimes over several weeks; the causes of this are obscure.

The behaviour of the larval bands offers some peculiarities owing to the relatively feeble degree of gregariousness, especially in the case of smaller and less dense bands. Nevertheless, the extremely careful and interesting observations by Kiritchenko have shown that the behaviour of the Italian Locust in the hopper stage depends on temperature as closely as in other locusts (some figures and other data have been quoted in Chapter IV, p. 80).

The larval development occupies from 30 to 43 days, according to the conditions. It is very interesting that Plotnikov (1926) observed a supplementary, sixth, larval stage in the females of *Calliptamus* in Turkestan, but Dovnar-Zapolsky insists that both sexes have only five larval stages. It is not impossible that the two authors had different species of *Calliptamus* before them, or that the number of larval stages may vary.

After the insects reach the adult stage, the swarms disperse. This is observed, to a certain degree, in all other locusts, but in them the swarms become dense again after a few days; this does not happen in *Calliptamus*, and its swarms, if formed, are always very loose. Accordingly, there are no regular migrations, only flights of loose groups of locusts extending over relatively narrow limits and definitely dependent on wind.

The feeding habits of *Calliptamus* are peculiar. Kiritchenko found that the principal food of the hoppers in the first stage consists of *Artemisia austriaca* and two species of *Achillea* (*A. setacea* and *A. nobilis*); other plants definitely preferred by the hoppers in the later stages are *Salvia aethiops*, *S. nemorosa*, *Carduus* (3 species), *Onopordon acanthium*, *Verbascum* (3 species), *Convolvulus arvensis*, *Datura stramonium*, and *Sisimbrium sophia*. This list is remarkable for a complete absence of any Gramineæ; indeed, even the most common of them are recorded by Kiritchenko only as eaten in exceptional cases; this constitutes a very sharp distinction between *Calliptamus* and the majority of ACRIDIDÆ, in which Gramineæ are the staple food.

As in other ACRIDIDÆ, the range of food plants increases with the growth of the hoppers, but their main tastes remain unchanged.

PERIODICITY

According to Plotnikov (1926), in Turkestan there seems to be a ten-years' cycle of *Calliptamus*, but it is difficult to see the reasons for this. There are no definite data for connecting outbreaks of the species with certain meteorological conditions, though the last outbreak (1924–25) in the Ukraine and in Western Siberia may have depended on abnormally dry and hot seasons. The ending of outbreaks very often happens as a result of epidemics of *Empusa grylli*, to which *Calliptamus* is particularly susceptible.

The problem of phases in *Calliptamus* remains obscure. Baranov (1925) has described, under the name *anachoretus*, a solitary form from the environs of Belgrade, but without giving any observations on the connection of this form with the swarming one; it is highly probable that *anachoretus* is simply another species. A study of phases in *Calliptamus* must offer great difficulties, since the habits of the swarming phase (if it is distinct) are not strongly pronounced, and this makes it probable that differences between the phases, if they exist, are very small.

ECONOMIC IMPORTANCE AND CONTROL

While *Calliptamus* is only very occasionally a swarming species, its ability to breed on cultivated lands and in their immediate vicinity makes it a very dangerous pest; it attacks mainly miscellaneous crops, such as vegetables, potatoes, tobacco, lucerne, cotton, etc., but it does not leave corn crops untouched. With regard to cotton in Turkestan and Persia, it has been found that the best cultivated crops suffer most, since where there are weeds in the fields, the locusts attack these first and the cotton plants afterwards, while good plantations free from weeds are destroyed immediately.

In any case, the Italian Locust cannot be said to constitute anywhere more than an occasional serious pest, and nowhere is it the sole cause of a special locust problem.

The control of *Calliptamus* is very easy from the technical point of view, if poison baits are used ; bearing in mind the special attraction of the species to *Artemisia*, it would be interesting to try and find the active substance in this plant and use it as an attractant in baits. A study of artificial ecological conditions caused by overgrazing in South Russian steppes would also be very important from the point of view of preventing the spread of this pest.

CHAPTER XVI

SOLITARY GRASSHOPPERS AND THE GRASSHOPPER PROBLEM IN SIBERIA AND NORTH AMERICA

The following chapter is devoted to a number of injurious species of Acrididæ having certain features in common, in that though they do not possess definitely developed swarming habits (except when appearing in very abnormally large numbers), they are able to multiply rapidly and to become serious pests of local importance. While species of similar characteristics may be met with in almost any country, only those of the temperate regions of the Northern hemisphere are at present sufficiently well known to permit a general discussion of them. Indeed, it is mainly in Canada and the United States on the one hand, and in Siberia and Eastern European Russia on the other, that grasshoppers of this kind play a fairly constant and sometimes highly important part in local economics. These two groups of countries are therefore discussed more particularly here. Other grasshoppers with non-swarming habits, peculiar to subtropical and tropical countries, will be discussed later (Chapter XVIII), while the grasshoppers of Argentina (locally called *tucuras*, see Bruner, 1898) which are very similar in their habits to those discussed in this chapter, must be left out altogether, owing to the lack of any reliable information on them.

No attempt is made to give here complete information on all species of grasshoppers able to become injurious in North America and Siberia, but only on those that can be regarded as more or less regular pests. Indeed, the literature includes records of a great many more injurious species than are discussed here, but it must be realised that nearly all Acrididæ, except a few of peculiar feeding habits, are potential pests, in the sense that they will feed on crops when the opportunity arises. To include all existing records would involve descriptions of practically all the species of Acrididæ known from North America, Siberia, and Europe, and this would be beyond the scope of the present book.*

Solely for the sake of convenience, the sequence of the species in this chapter is in accordance with their systematic position.

The Siberian Grasshopper (*Gomphocerus sibiricus*, L.).

Adult Insect (Fig. 94).—Brown, or olive-green, with indistinct dark markings. Antennæ of the male clavate, in the female also somewhat incrassate apically. Pronotum of the male strongly, in the female slightly, inflated in its anterior portion ; lateral pronotal keels pale, obtusely angulate. Elytra

* A good review of species that have been recorded as doing damage in various countries, with a bibliography, is given by Zacher (1926).

in the male longer than the body, in the female shorter than it, with an indistinct pale spot near the apex. Front tibiæ in the male with a strong pear-shaped inflation, in the female normal. Hind tibiæ yellowish, or reddish. Length, male 19–20 mm., female 19–25 mm. ; elytra, male 13–15 mm., female 11–15 mm.

Hoppers.—In the first stage, the hopper is greenish-brown, or brown, with the antennæ 13–14-jointed ; length about 5 mm. In the second stage rudiments of elytra and wings become distinct, antennæ are 16–19-jointed. Antennæ of the third-stage hopper consist of 21 and more joints. Hoppers of the last, fourth, stage have wing rudiments reaching to the middle of abdomen and are about 20 mm. long.

Egg-pod.—Oval in shape, somewhat thicker in the middle, 8–12 mm. long and about 6 mm. in diameter. Walls thin, made of earth, moderately strong. Inner cavity single-chambered. Number of eggs 7–10 ; they are whitish-grey, about 5 mm. long and 1·2 mm. in diameter, placed in three rows. There is no lid, but a porous stopper (Berezhkov, 1923).

Distribution and Ecology.—The area of distribution of the Siberian grasshopper justifies its name, since the species inhabits nearly the whole of Siberia, except the most northern zone, ranging from the Pacific Ocean to the Ural Mountains and even somewhat beyond them into North-Eastern European Russia. Further westwards and southwards this grasshopper occurs only sporadically in mountains—in the Caucasus, Balkans, Alps, Appenines, Pyrenees, and in the highest parts of the mountains of Central Spain ; these "islands" populated by the species represent relics of a wide continuous area occupied by this species shortly after the Glacial epoch when the Siberian steppes with their typical fauna stretched right across the whole of Europe.

Fig. 94.—Siberian Grasshopper, ♂, enlarged (original).

The ecological requirements of the Siberian grasshopper are as yet very little known, since all available observations apply not to the main continuous area of distribution of the species but to its mountain habitats which may not be typical. Speaking generally, however, the species is connected with the forest-steppe zone and partly with more northern division of the steppes, and seems to be rather xerophilous in its habits, though it avoids high summer temperatures.

Life History.—The conditions preferred for oviposition have not been studied, but Russian authors point out a tendency on the part of the Siberian grasshopper to lay its eggs in hard soils and in places where the covering of vegetation is not dense ; low-lying, damp places are avoided.

Hoppers, after hatching, remain at first in small groups, but soon disperse, even if their numbers are large and the groups of considerable dimensions. There are only four hopper stages, and the larval development occupies 25–30 days. Four days after the final moult, the adults pair, and two days later the first egg-pod may be laid (Bezrukov, 1922).

The behaviour of the hoppers and adults has never been adequately studied. In cases of great outbreaks, swarms of flying individuals may form, and irregular flights, or rather swarms, drifting with the wind may be observed.

Economic Importance.—As a pest of corn crops in the steppe zone of Siberia, this species is of enormous importance, since on its numbers depends the annual harvest in an area of vast size and of high productive capacity. Since the food of the grasshopper consists almost exclusively of Gramineæ and the whole development occurs in the immediate vicinity of cultivated fields, or amongst them, the damage done, even in normal years, must be considerable, while in the years of outbreaks the losses may be enormous. The crops mainly attacked are wheat, barley, and oats ; rye is damaged only occasionally, and other cultivated plants still more rarely.

Apart from destroying cultivated plants, the Siberian grasshopper must be of importance as a grass feeder in grazing lands, but this side of the problem has never been studied.

The Dark-winged Grasshopper (*Chorthippus scalaris*, F.W., = *Stauroderus morio*, F.).

Adult Insect (Fig. 95).—Under medium size, slender. Antennæ fine and long. Face in profile strongly oblique. General coloration brown, or dark-green, with two velvety-black stripes along the pronotum ; the latter with the lateral keels pale, rounded-incurved. Elytra brownish, the apex black ; in the male the elytra are expanded, with regular venation. Wings dark-brown, almost black ; their main veins incrassate ; transverse veinlets regularly spaced. Hind tibiæ reddish-brown. Length, male 18–22 mm., female 22–29 mm. ; elytra, male 18–20 mm., female 17–20 mm.

Fig. 95.—Dark-winged Grasshopper, male, enlarged (original).

Hoppers.—No description exists.

Egg-pod.—Oval, thicker in the middle ; 7–9 mm. long and about 4 mm. in diameter. Walls almost leathery, with a slight admixture of earth, thin, moderately strong. No lid. Eggs 5–10 in number ; they are yellowish, 4 mm. long and 1 mm. in diameter, placed in three rows (Bezrukov, 1923).

Distribution and Ecology.—The area of distribution of this species entirely covers that of the Siberian grasshopper and extends beyond it both westwards and southwards, so that in Europe it occurs not only in the mountains, but also in the plains. Ecological data on this species are very meagre, but it appears to be more mesophilous than the Siberian grasshopper, and is connected with moderately rich grasslands.

Life History and Economic Importance.—Eggs are laid in relatively soft soils. Mass hatching occurs about a fortnight later than in the Siberian grasshopper. The number of larval stages is four. The economic importance of the Dark-winged grasshopper is very great. Though generally second in

numbers to the Siberian grasshopper, it is sometimes even more numerous, causing great damage to corn crops in Siberia and the regions on both sides of the Ural Mountains (Filipjev, 1926).

The Cross-bearing Grasshopper (*Arcyptera microptera*, F. W., *A. flavicosta*, Fisch.).

Adult Insect (Fig. 96, A).—Of medium size, rather robust. Coloration yellowish-brown, with grey and pale-yellow pattern. Pronotum above dark grey ; lateral keels angulate inflexed, pale yellow. Elytra in the male extend beyond the hind knees, in the female just reach them ; they bear grey spots and a yellowish line near the front margin. Hind femora with indefinite grey spots. Hind tibiæ red. Length, male 19–22 mm., female 24–29 mm. ; elytra, male 13–18 mm., female 17–21 mm.

Hoppers.—Grey, with dark dots. Along the head, pronotum, and abdomen there is a whitish line between two black bands ; in the later stages a whitish, cross-shaped pattern on the pronotum becomes visible, while the longitudinal line becomes less sharply defined. Hind femora with three whitish bands ; hind tibiæ with a white ring.

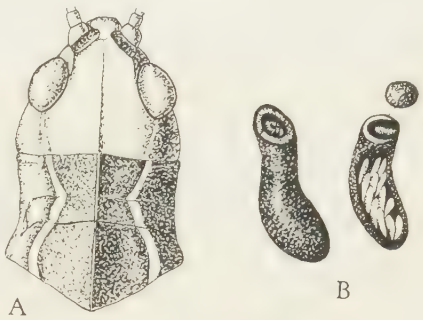

Fig. 96.—Cross-bearing Grasshopper.—A, head and thorax, enlarged (original).—B, egg-pods, nat. size (after Znamensky).

Egg-pod (Fig. 96, B).—Cylindrical, somewhat curved, thickened to the lower end, which is rounded. Length, 18 mm. ; diameter, 7 mm. Walls hard, made of earth. Lid like a disc, semi-lunar in cross-section. Inner cavity without a porous mass above the eggs. Eggs dull-yellowish, 5 mm. long and 1·5 mm. in diameter, 10–15 in number, placed in three rows, forming an angle of about 45° with the walls (Bezrukov, 1923 ; Vorontsovskii, 1924).

Distribution and Ecology.—The area of distribution of this grasshopper forms a narrow strip, extending from Spain, through Southern France, Italy, Southern Austria, the Balkans, and Hungary into the South Russian steppes, where the strip becomes broader and stretches into the steppe and forest-steppe zones of Siberia. In the Caucasus and Central Asia, this grasshopper penetrates relatively far to the south, but is always connected with the foot-hills bearing vegetation of the steppe type.

This species is everywhere an inhabitant of dry steppes with short grass vegetation ; where it penetrates into semi-desert country, it occupies depressions covered with grass.

Life History and Economic Importance.—The eggs are normally laid in dry hard soils, always virgin ones. Hatching occurs earlier than in the majority of Russian Acrididæ, and this is one of the earliest of the injurious species to appear. There are four larval stages, and the period of development occupies about 30 days (Moritz, 1915). The hoppers, even when numerous, do

not form bands and lead each an independent life, though their various actions (feeding, climbing the plants, etc.) occur simultaneously, being regulated by temperature (Modestov, 1921).

The economic importance of this species is determined by its connection with virgin steppes, which makes it really dangerous only in regions where there are still large areas of uncultivated lands and relatively small cultivated ones. Over the greater part of European Russia this condition is a thing of the past, but in Western Siberia and, particularly, in the more recently colonised districts of the Kirghiz steppes, conditions are still very favourable to this grasshopper, and it sometimes becomes the most injurious species.

The Clear-winged Grasshopper (*Camnula pellucida*, Scudd.).

Adult Insect (Fig. 97).—Of medium size, pale brown, with blackish markings. Face in profile slightly oblique. Pronotum above flat, with the lateral keels continuous, practically straight; median keel low; often there are pale stripes along the lateral keels; lateral lobes with a large black spot in the anterior half and a pale one in the posterior. Elytra of the male extend beyond the abdomen, in the female they reach its end, with a pale stripe

Fig. 97.—Clear-winged Grasshopper, enlarged (after Treherne and Buckell).

Fig. 98.—Clear-winged Grasshopper; first stage, enlarged (after Treherne and Buckell).

along the anal vein, in front of which are numerous irregular dark spots. Wings hyaline. Hind femora with oblique dark fasciæ. Hind tibiæ yellowish. Length, male 17–21 mm., female 21–28 mm.; elytra, male 16–19 mm., female 19–24 mm.

Hoppers (Fig. 98).—Hoppers of the first stage possess a very typical and fairly constant coloration, being dark grey, almost black, with conspicuous broad white stripes on the sides of the head and lateral pronotal lobes. In the later stages, the colour and pattern is variable, the white stripes usually disappearing (Treherne and Buckell).

Egg-pod.—There is no proper description of the egg-pods, which are stated by Somes (1914) to be rather short, stout, considerably curved, and not firmly cemented. Eggs are about 4 mm. long and 1·5 mm. in diameter; their number vary from 10 to 30.

Distribution and Ecology.—The species is widely distributed in North America, its southern limit being in northern Pennsylvania, Indiana, and Illinois, while further west it reaches Nebraska, New Mexico, and California (Blatchley, 1920).

Ball (1915) describes its breeding grounds in Utah as dry, strongly alkaline

places with a scanty vegetation of scattered stalks of *Atriplex*, *Distichlis*, and *Hordeum jubatum*.

In British Columbia this species is known as the "Roadside Grasshopper," since it has the habit of selecting dry, bare roadsides for oviposition, and this defines its ecological characteristics. Indeed, this preference for artificially bared grounds makes it somewhat difficult to assign to its proper natural habitat. In British Columbia it is very common and numerous on bare open ranges, especially those much overgrazed, *i.e.* under conditions that are due to the action of man; the same ranges, if fenced off from cattle, soon produce a relatively dense vegetation, and the Clear-winged Grasshopper disappears. It must be assumed that the normal habitat of this species is denuded spots in very dry grassland, and that agriculture brings about various changes in habitat that are favourable to the species (Treherne and Buckell).

Life History.—Hatching in British Columbia occurs from the middle of May to the middle of June, though it may continue throughout July. The hoppers of the first two stages, if hatched in sufficiently large numbers, concentrate over narrow areas and exhibit marked gregarious and migratory habits; this may also be observed in the later stages (owing to this habit, the species is called in some of the Western United States "the Warrior Grasshopper"). When, however, the hoppers are scattered, though numerous, they reach the adult stage without wandering. The adults also are inclined to undertake flights in swarms, though they are never dense, and the flights are not regular and do not extend over great distances. This species may therefore be considered to be partly gregarious.

Numerous observations by Parker (1924) on the behaviour of the Clear-winged Grasshopper in relation to temperature have been already mentioned (p. 69).

Economic Importance.—The normal food of the hoppers consists entirely of Gramineæ, and during outbreaks, grain crops suffer severely. Of still more importance is this grasshopper in its relation to pasture lands, and in British Columbia it is considered the main species concerned in the depletion of grass vegetation of ranges. Apart from grain crops, various vegetables are readily attacked, when the opportunity arises, but potatoes and beet are left to the last; lucerne, according to Treherne and Buckell, is not damaged, but Somes (1914) says that this grasshopper eats lucerne both in cages and in the field.

The Flightless Grasshopper (*Podisma pedestris*, L.).

Adult Insect (Fig. 99, A).—Of medium size, clumsy. General coloration pale brown, with yellow and black markings. Pronotum above practically flat; median keel very feeble, no trace of the lateral keels. Lateral pronotal lobes yellow below, higher up with a shining black stripe. Prosternum between the bases of the front legs with a straight conical spine. Elytra rudimentary, oval, scarcely reaching beyond the first abdominal segment; wings absent, though fully winged individuals occur exceptionally. Hind femora above with two indistinct dark spots, below and on the inside red.

Hind tibiæ blue. Abdomen of the male with alternating yellowish and black transverse stripes. Length, male 15–22 mm., female 22–30 mm.; elytra, 3–5 mm.

Hoppers.—In the first and second stage, coloration pale brown with dark chocolate spots. Head very large, with strongly projecting eyes. Antennæ with 13–14 joints, the base of each joint paler than the rest. Hind tibiæ with a whitish ring. Hoppers of the later stages have rudiments of both elytra and wings, but the latter disappear at the final moult.

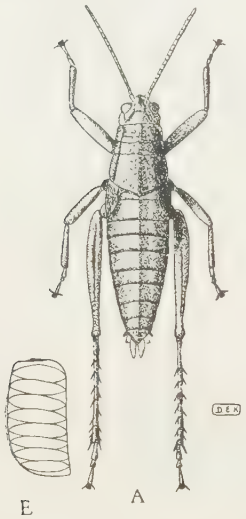

Fig. 99.—Flightless Grasshopper, natural size.—A, adult female (original).—E, diagram of the egg-pod, nat. size (after Bezrukov).

Egg-pod (Fig. 98, E).—Irregularly oval, almost prismatic, slightly compressed and curved, about 13 mm. long and 5 mm. in diameter. Walls thin, made of earth, moderately strong, separable from the eggs with difficulty. There is no lid. Eggs 18–32 in number, about 4·5 mm. long and 1·2 mm. in diameter; their outer cover with tubercles and pits, rusty in colour; the eggs in the pod are placed in four rows, practically parallel to its bottom (Bezrukov, 1923).

Distribution and Ecology.—The area of distribution of this species occupies a great part of Siberia and of Europe, its southern boundary coinciding with the northern limits of the steppe zone. In Western Europe this grasshopper occurs in Germany and Austria, while farther westwards it is restricted to mountains. In Asia it does not penetrate into Turkestan, but extends into Mongolia.

As regards ecology, the Flightless Grasshopper is characterised by its decidedly phytophilous habits, since it lives mainly on plants, not on the ground. The most favoured habitats are those with a rich mesophilous vegetation, often margins of forest, or clearings in forest with shrubs, on which, as well as on trees, this grasshopper often occurs.

Life History and Economic Importance.—Very little is known about the bionomics of this species. There are, apparently, four larval stages.

The area where the Flightless Grasshopper is injurious coincides in Siberia with the northern parts of the forest-steppe zone, where it sometimes appears in great numbers and attacks grain crops, as well as other cultivated plants. Particularly important does it become in Eastern Siberia (Transbaikalia), where another species of a nearly allied genus, *Prumna primnoa*, F. W., occurs with it and also causes damage, particularly in vegetable gardens (Engelhardt, 1925).

The Lesser Migratory Grasshopper (*Melanoplus mexicanus atlanis*, Riley).

Adult Insect (Fig. 100).—Of medium size, reddish-brown, or dark olivaceous, with a blackish pattern. Pronotum above practically flat; median keel

distinct only in its posterior half; no lateral keels; transverse sulcus deep and the pronotum at this point somewhat depressed; lateral lobes with a black spot. Elytra extending beyond the hind knees by 2–3 mm., with a series of dark spots along the middle. Prosternum between the front legs with a conical blunt spine. Male cerci compressed, about twice as long as broad, obliquely rounded. Male subgenital plate notched at the apex. Hind femora with two oblique dark fasciæ. Hind tibiæ reddish, glaucous, or bluish. Length, male 17–21 mm., female 16–27 mm.; elytra, male 15–21 mm., female 15–22 mm.

Hopper of the First Stage.—Dull greyish-brown, dotted with black, sometimes with a pale median stripe above. Hind femora dark, with pale fasciæ. Antennæ 12-jointed. Length 4–5 mm.

Hopper of the Second Stage.—Slightly paler than the first stage. A subquadrate black mark behind the eyes, extending across the pronotum rather distinct; a pale more or less crescent-shaped streak at lower margin of that mark. Fasciæ of hind femora more distinct and broader. Antennæ 15-jointed. Length 6–8 mm.

Hopper of the Third Stage.—Distinctive markings of the previous stages still more pronounced. Distinct rudiments of elytra and wings. Antennæ 17–18-jointed. Length 9–12 mm.

Hopper of the Fourth Stage.—Dorsal surface of the body very dark. Markings very distinct, black and almost white. Rudiments of elytra are turned upwards, dark; hind wings each with a white spot near the middle. Antennæ 21-jointed. Length 13–15 mm.

Fig. 100.—Lesser Migratory Grasshopper, enlarged (after Treherne and Buckell).

Hopper of the Fifth Stage.—Rudiments of wings reaching beyond the hind margin of the second abdominal segment. Antennæ 23–24-jointed. Otherwise similar to the preceding. Length 16–20 mm. (Description after Herrick and Hadley, 1916.)

Egg-pods.—Shape variable, cylindrical or more or less curved, thickened towards the lower end. Walls thin, made of earth. Stopper formed of a spongy mass, long, occupying $\frac{1}{4}$ to $\frac{1}{2}$ of the pod. Number of eggs varies from 5–18; they are 4·3–4·4 mm. long, and 1·2 mm. in diameter, yellowish; chorion shallowly pitted.

Distribution and Ecology.—The species is one of very wide distribution, ranging from the tropical lowlands of Mexico (where it is represented by the typical subspecies) throughout all the United States (except peninsular Florida and California west of the Sierra Nevada) to Southern Canada, and extending on the Pacific Coast into British Columbia as far north as the Chilcotin district (Hebard, 1925).

The ecological conditions under which this species is particularly abundant are stated by Herrick and Handley in New York State to be somewhat circumscribed. Its habitat seems to be open grassland, with short wiry grasses and fairly compact sandy soils; the sandy knolls and ridges abounding in

such places are favourite egg-laying grounds, but in areas where the sand is loose it is less numerous. Similar conditions are recorded for this grasshopper from other States, while in British Columbia it is especially at home in the bunch-grass prairie, which " may be pictured as a plain lightly covered with hillocks of grass growing normally fifteen inches to two feet in height " (Treherne and Buckell).

Such are the ecological conditions most favourable to the species, but it occurs also in a wide variety of habitats, exhibiting a considerable adaptability.

Life History.—The hoppers hatch in New York State in April or May, in British Columbia in the middle of May or later, even up to August. The larval period is rather prolonged compared with other grasshoppers, occupying about six weeks (Herrick and Hadley estimated it at as much as 59 days, but this seems too long). The hoppers are typically solitary in their behaviour and inclined to climb plants more than other species ; this also applies to the adults. The latter do not form dense swarms, but during very severe outbreaks, definite attempts at migration of loose swarms have been observed on many occasions, indicating that this species has some tendency to become migratory, if its numbers are large and its swarms reach sufficient density. Oviposition begins in New York State in the middle of July and continues for six weeks or more. The eggs normally hibernate, but Herrick and Hadley have found several old records of a second generation in a year.

Economic Importance.—Very severe outbreaks of this species are definitely known from a number of States in the U.S.A., as well as from Canada, and the species must be considered an extremely dangerous pest. Its importance is still more emphasised by its ability to acquire migratory habits during exceptionally severe outbreaks. Indeed, there are strong reasons to suspect that *M. atlanis* has an intimate relation with the dreaded *M. spretus*, Walsh (Rocky Mountain Locust), which devastated large areas of the United States in the last century, but disappeared not only as a pest, but even as a species, about fifty years ago, only isolated specimens, not always typical, having been met with since. The differences between *atlanis* and *spretus* are very small and only relative (Somes, 1914), *spretus* being larger, with longer elytra and a more strongly constricted pronotum. There are also minute differences in the male genitalia, but this character is not absolutely stable in *atlanis*. It will be noted that these differences between the two insects are of the same kind as those observed between the swarming and the solitary phase of some true locusts (see pp. 147, 159), and the suggestion that *spretus* is only the swarming phase of *atlanis* seems highly probable, even to pure systematists (Hebard, 1925), while a number of economic entomologists in America are also in favour of this hypothesis. It would seem, therefore, that *spretus*, as a swarming phase, cannot now develop as it used to do in the earlier periods of American agriculture, and the reason for this may be seen in disturbances in the ecology of its breeding areas. Unfortunately, the excellent work on the Rocky Mountain Locust accomplished by the United States Entomological Commission, while resulting in a fairly accurate determination of the geographical position of permanent breeding areas of *spretus*, did not include any detailed investigations

of the natural conditions of the actual breeding grounds. Later authors have ascribed the disappearance of the Rocky Mountain Locust to the advance of agriculture which destroyed its breeding grounds, but no attempt has ever been made to determine exactly what kinds of habitats were actually destroyed in the Rocky Mountains to such an extent that a species (or a form of species) of an insect disappeared within living memory. The problem is one of unusual scientific interest, while its economic bearings are also very important. Indeed, it seems very disputable that agriculture really brought about such a thorough change in the environment that the breeding of *spretus* became an absolute impossibility. In fact, on the basis of the phase theory, I believe that its reappearance would be not surprising, provided that some conditions—absolutely unknown to us at present—were to stimulate the development of *atlanis* beyond the status of a semi-gregarious species, which it attains fairly often. The same idea is expressed by Hebard (1925), who says: "Since the subsidence of the last and greatest outbreak in the 70's, *spretus* has become one of the rarest of all forms even in the regions where it was supposed to have a permanent habitat. When it will again burst forth to devastate not only counties, but even States, is purely a matter of conjecture."

Fig. 101.—Red-legged Grasshopper, about natural size (after Lugger).

In view of all these considerations, it is very surprising that the problem of *atlanis* and *spretus* does not attract any attention from entomologists in America. A thorough study of the conditions in the former breeding grounds of *spretus*, their comparison with the historical evidence as to the conditions there fifty years ago, coupled with laboratory breeding experiments under various conditions (including overcrowding)—all these might throw some light on the problem, which is surely a most fascinating one, apart from its great practical interest. It is to be feared, however, that, as usual, research will be stimulated only by realisation of the worst possible situation, when it will be too late.

The Red-legged Grasshopper (*Melanoplus femur-rubrum*, DeG.).

Adult Insect (Fig. 101).—Size medium, but variable. Coloration reddish-brown, the pronotum lighter on the disc than on the lower parts of the lateral lobes. Pronotum little depressed at the hind sulcus; median keel feeble, but more pronounced than in *M. atlanis*. Prosternum between the front legs with a cylindrical spine, which is very blunt, almost inflated, apically.

Elytra extending beyond the hind knees, with some small brownish spots. Hind femora with faintly indicated dark fasciæ. Hind tibiæ always red. Male cerci fairly long, distinctly tapering to the apex, which is obliquely truncate. Length, male 16–23 mm., female 18–29 mm. ; elytra, male 13–21 mm., female 15–23 mm.

Hoppers and **Egg-pods** not described in any detail.

Distribution and Ecology.—One of the most widely distributed grasshoppers in America, occurring commonly over the entire United States, penetrating into Mexico as far as Vera Cruz and into Canada as far as Halifax, Nova Scotia in the east and the Chilcotin District of British Columbia in the west (Hebard, 1925).

In its ecological requirements, the Red-legged Grasshopper is decidedly mesophilous, being found always among more or less dense grasses and weeds, especially close to cultivated fields and in them ; in more arid portions of its area, it occurs only near water.

Life History.—Similar to other species of the genus, but hatching and reaching the adult state later than most of its congeners. In its habits the Red-legged Grasshopper is purely solitary, though exhibiting a certain tendency to flights during unusually severe outbreaks (Somes, 1914).

Economic Importance.—From the economic point of view this species must be of considerable importance even in normal years, since it is always present in large numbers and feeds on a variety of cultivated plants. During outbreaks, various crops suffer severely, but the damage is always localised.

The Differential Grasshopper (*Melanoplus differentialis*, Uhl.).

Adult Insect (Fig. 102).—Larger than other species of the genus and heavily built. Coloration testaceous, or olivaceous, sometimes yellowish, with but a feebly developed dark pattern on the lateral pronotal lobes. Elytra uniformly coloured, reaching or somewhat surpassing the hind knees. Hind femora stout, without fasciæ, but on the outside with a black pennate pattern. Hind tibiæ olivaceous. Length, male 28–34 mm., female 34–44 mm. ; elytra, male 29–32 mm., female 32–35 mm.

Fig. 102.—Differential Grasshopper, natural size (after Lugger).

Hoppers.—No proper description exists.

Egg-pod.—According to Hunter's (1899) figures and somewhat vague description, the egg-pods of this species are provided with relatively brittle walls, which easily break off when disturbed. Eggs about 100 in number, not very regularly arranged, 5 mm. long and 1·25 mm. in diameter, bright yellow ; chorion with ridges forming a hexagonal pattern.

Distribution and Ecology.—According to Hebard (1925), the Differential Grasshopper is known only from a few localities on the Atlantic coast of North America and was probably introduced there by man, while the main area of distribution is farther west, the eastern limits being in Indiana, Kentucky,

and Tennessee. The northern limits are Douglas Lake in Michigan, Wisconsin, Minnesota, South Dakota, and Wyoming. It is apparently largely absent from the Great Basin, but is known from Colorado, New Mexico, Nevada, Arizona, California, and penetrates southwards into Mexico as far as Vera Cruz.

Ecologically the species seems to be similar to the Red-legged Grasshopper, avoiding very dry habitats and showing a decided preference for cultivated lands. Lucerne fields are particularly suitable for its development (Hunter, 1898), though the eggs are laid, apparently, mainly at their margins and on more or less bare spaces, but they are often placed close to the roots of plants.

Life History.—There are no particular differences from other members of the genus so far as the life history has been studied.

Economic Importance.—Preference for cultivated lands makes the Differential Grasshopper of particular interest to farmers, and the damage done by it is very often considerable. In the Mississippi valley, this species has been noticed to develop particularly after big floods, when cultivated lands have had to be abandoned for one or two seasons, thus creating conditions favourable to the eggs (Morgan, 1901). In the lucerne fields of Kansas, the damage was considerable and regular until the practice of disking was widely applied.

The Two-striped Grasshopper (*Melanoplus bivittatus*, Say).

Adult Insect (Fig. 103).—Rather large and robustly built. Coloration dull olive-brown or greenish-yellow, without spots, but with a distinct pale stripe on each side of the head behind the eyes, continued along the sides of the pronotal disc and along the edge of the folded elytra. Hind femora sometimes with ill-defined dark fasciæ; knees black. Hind tibiæ yellow, bluish, or red. Length, male 23–29 mm., female 29–40 mm.; elytra, male 16–22 mm., female 19–26 mm.

Fig. 103.—Two-striped Grasshopper, natural size (after Lugger).

Hoppers and Egg-pod not described.

Distribution and Ecology.—According to Hebard (1925), this species occurs everywhere in the United States except the south-eastern portion, and is confined mainly to irrigated areas in the arid regions of the West. In California it is extremely scarce or absent except in the northern parts. Its range extends northwards to Newfoundland, Quebec, Southern Manitoba, Saskatchewan, Alberta, and British Columbia, while southwards it penetrates into Mexico.

As regards the ecology of the species, it appears to require a certain degree of humidity, preferring low-lying lands, margins of woodlands, and shaded mountain slopes (Herrick and Hadley, 1916), but it is also widely spread in

various cultivated habitats, and especially in lands that have been under cultivation and then deserted for a number of years (Somes, 1914).

Life History.—The Two-striped Grasshopper prefers hard soil for oviposition such as roadsides, etc., though the eggs are not infrequently laid in stubble. As regards other points of the life history, there are apparently no appreciable differences from other members of the genus, though this may be due simply to an insufficient knowledge of the habits of all of them.

Economic Importance.—This species is apt to increase in numbers very rapidly, perhaps because it is always one of the commonest and numerous species in North America. It mainly attacks cereals, but other crops, including lucerne, also suffer much from it.

Other Species of Grasshoppers

Apart from the species discussed above, there are a good many more, both in North America and in Russia, that may become numerous and injurious occasionally. Since, however, outbreaks of them are very irregular and rare, it would scarcely serve any useful purpose to give descriptions of them, the more so as their bionomics are practically unknown. There is no doubt, also, that a certain percentage of species that have been recorded in the literature as injurious should be excluded from lists of pests. It is not an uncommon practice, when an outbreak of grasshoppers is in progress, to make a full list of the species seen in the field and credit the damage to all of them, while there are undoubtedly many species which, though numerous, do not feed on cultivated plants. Several such species are known in Russia; for instance, *Psophus stridulus*, L., has always been included amongst pests of grain crops, but, according to Berezhkov (in Filipjev, 1926), it does not eat Graminaceous plants at all.

The Grasshopper Problem in North America

As we have seen in Chapter IX (p. 216), the organisation for controlling grasshoppers should differ in principle and in details from that required for swarming locusts, this depending on differences in their habits and in the economic importance of the two groups. The organisation for the control of grasshoppers can and should be based on the concerted action of farmers themselves, and this form of organisation has attained a high degree of perfection in the United States, where co-operative action against grasshoppers is often taken on a large scale and with great success. The technique in use is mainly poisoned baits, but hopper-dozers and hopper-catching machines are also in use.

While the question of the suppression of outbreaks may be considered very successfully solved in the majority of the States, there are certain aspects of the problem there to which this does not apply, for the important problem of prevention has been hardly ever studied. Most American authors, it is true, recommend certain agricultural methods, which, in their opinion, should serve to reduce the numbers of grasshoppers and prevent mass outbreaks, but all these are based on theoretical considerations, not on experimental work,

because no such work on the influence of various methods of agriculture on the development of grasshoppers has ever been done on a proper scale. Moreover, there is scarcely any real basis for such work, which must begin with a thorough ecological study of each species concerned, while not a single one of the American grasshoppers has been made the subject of such an investigation. To take only the most striking case—that of *Melanoplus atlanis*—its ecology in the whole area of its distribution has never been studied, though this might throw some light on the extremely interesting and highly important problem of its relation to the Rocky Mountain Locust.

Ecology apart, there is no information even on the stages of development of the most important American grasshoppers, with the result that field observations on the early stages of various species are impossible ; the same difficulty would arise in ecological studies for the same reason, and the work of making good morphological descriptions of all stages of development of all the more common species is urgent. General studies on the life history and habits of each species must follow, and only then will it be possible to begin experimental work with a view to ascertaining the agricultural methods that are favourable, or otherwise, to a certain species. Until the latter work brings some definite results, there is little reason to recommend one or the other measure as likely to check grasshoppers.

Conditions in Canada are in part very similar to those in the United States, where there are more densely populated provinces with agriculture at a high level, but differ in the less settled provinces where stock-raising predominates over agriculture. For example, in parts of British Columbia, the ranges are apt to become secondary breeding areas for various species and constitute a menace to adjoining farm lands. While it is quite possible to deal with grasshoppers on the ranges, both by means of the usual methods and by applying certain ecological measures such as avoidance of overgrazing (Treherne and Buckell, 1924), there must be, apparently, some definite policy in the matter, and the problem should be dealt with on a large scale and not left to individual owners of ranges. A thorough knowledge of local conditions is necessary to evolve a satisfactory scheme ; meanwhile it is not possible to do more than offer the suggestion, in a very generalised form, for some kind of legislation providing for the prevention of grasshopper outbreaks on pasture lands. There is no doubt that practical measures to that effect can be recommended in each district only after a thorough study of the local species of grasshoppers and their ecology and connection with the methods of managing ranges. A very sound basis for such studies has been laid by Treherne and Buckell.

The Grasshopper Problem in Russia

Difficulties in suppressing outbreaks of grasshoppers in Russia (above all, in Siberia, where these insects are particularly important) are very great, depending as they do on the very large areas concerned and, still more, on the low standard of education of the peasants and correspondingly great obstacles to the success of co-operative campaigns. Recent years have, however, seen great advances in that direction, and there is little doubt that future outbreaks

of grasshoppers can be dealt with in a perfectly satisfactory way, as regards their suppression and prevention of damage.

Very different is the position with regard to prevention of outbreaks, since the base of it—ecological knowledge—is almost absent. There are some vague indications that the present system of agriculture in Siberia, where lands are left to lie fallow for several years without being disturbed, and this in the immediate vicinity of crops, is highly favourable to the development of some species, notably, of the Siberian Grasshopper. There is, however, no exact information on this point, and thorough ecological investigations are urgently wanted, to be followed by experimental work on the influence of various agricultural methods on different species of grasshoppers. In some respects this work will be easier in Russia than in America, since in the former country more attention has been paid to the stages of development of various grasshoppers, and for the majority of the injurious species they are all known, making field work possible. On the other hand, the ecological side of the problem is entirely untouched, and in this direction there is an enormous amount of work to be done if methods of prevention of outbreaks are to be found.

CHAPTER XVII

THE LOCUST AND GRASSHOPPER PROBLEM IN AUSTRALIA

Species of Australian Locusts and Grasshoppers

The study of the Australian Acrididæ, even from the purely systematic point of view, is still in its infancy, and our knowledge of the Australian fauna is only fragmentary. It is not surprising, therefore, that the available information on the injurious species is characterised by an extreme vagueness of specific determinations, and in some cases it is absolutely impossible to decide to which species certain data apply.

A careful analysis of various reports and articles in periodicals (there being not a single really scientific paper on locusts and grasshoppers in Australia) permits one to select a few species that seem to be more common as pests, and these will be described below. It must be realised, however, that the information is very fragmentary, and it is likely that several of these species are but very occasional pests, while, on the other hand, there may be other species equally, or more, injurious but overlooked, or misidentified locally. It is advisable, therefore, that in all future outbreaks more attention should be paid to correct identification of the species involved than has been the case in the past.

One of the species injurious in Australia (particularly in the sugar-cane areas of Queensland) is locally called *Locusta australis*, Br. W.; this is only a form of the Migratory Locust, *L. migratoria*, L., and it has been discussed above (see Chapter XI).

Next comes its relative, *Gastrimargus musicus*, F., which in the local literature is usually recorded under a wrong name, *Locusta danica* (Froggatt, 1910, etc.).

Another species very similar to the preceding is *Oedaleus australis*, Sauss., which is also incorrectly named locally *O. senegalensis*, Kr.

Apparently the species of most economic importance in Australia is the, so-called, "Wandering Plague Locust" (Froggatt, 1910), which it would be better to call the "Wandering Grasshopper," since it is not a true locust in its habits. Its scientific name is *Chortoicetes terminifera*, Walker (Sjöstedt, 1921, removed it incorrectly to a special genus, *Calataria*).

Mixed with the latter in the local literature are undoubtedly other species of the same genus and of the closely related *Austroicetes*, Uv. (which corresponds to Sjöstedt's incorrect interpretation of the genus *Chortoicetes*); it is, however, practically impossible to decide to which species certain papers refer.

One or two more species are mentioned in the local literature as occasionally injurious, but since even their correct scientific names remain obscure, it would not serve any useful purpose to repeat the information here.

THE WANDERING GRASSHOPPER (*Chortoicetes terminifera*, Walk.).

Adult Insect (Fig. 104).—Of medium size, rather slender. Face distinctly oblique in profile. Foveolæ of vertex distinct, impressed, elongate, narrowed in front. Pronotum slightly constricted in front of the middle, with a low median keel, but without the lateral keels. Elytra reaching beyond the hind knees, with thick, regularly disposed, oblique veinlets in the discoidal field, which is provided with a false vein that joins the radial vein about its middle. Coloration brownish; pronotum with a whitish X-shaped design; elytra with large brown or blackish spots; wings with a smoky spot at the apex; hind femora with dark bands; hind tibiæ reddish, with the base paler. Length, male 22–36 mm., female 28–33 mm.; elytra, male 22–26 mm., female 24–30 mm.

FIG. 104.—Wandering Grasshopper, natural size (original).

Hoppers.—Not properly described.

Egg-pods.—Also not described, but Gurney (1925) says that each contains 36 eggs on the average.

Distribution and Ecology.—Data on the distribution of the species are somewhat fragmentary. Sjöstedt records it from a number of localities in Queensland, Victoria, New South Wales, and Western Australia, so that it seems to be spread over the whole continent. Damage from it has also been recorded from nearly all the Australian States, but it must not be forgotten that in many cases the specific determination is doubtful. Thus, Newman (1924) described the bionomics and ecology of what he believed to be this species in Western Australia, but from the photograph of the adults he gives, it is clear that he had before him some species of *Austroicetes* (see below).

The eggs are laid (Gurney, 1925) on bare burnt patches on gently rising land, on roadways and trodden paths, *i.e.* always in hard undisturbed soil.

Bionomics.—The number of annual generations has been estimated by the same author (Gurney, 1908 and 1925) differently. From observations in New South Wales in 1908 he deduced that there were three generations, the first hatching during August, September, and early October; the second appearing during November and December; and the third in February and March; the eggs laid by the last generation hibernate. In 1925 Gurney recognised only two generations, the first hoppers appearing in spring during September to November; the first winged swarms in December to February; the second generation of hoppers from January to March, and second adult swarms in March to May. It seems that he may have been right in both cases, since the generations are not clearly defined, but overlap to a great extent, and their number must depend on weather conditions of the year. In any case, there is a long winter embryonic diapause through about five winter months, while in the summer, generations follow each other without interruption.

No very definite information exists with regard to the habits of the Wandering Grasshopper, but it appears that its larval bands hardly undertake any mass movements, while adult swarms do not make regular migrations, only short drifting flights.

THE PLAINS GRASSHOPPERS (*Austroicetes* spp.).

The Species Involved.—Froggatt applied the name "Smaller Plain Locust" to *Austroicetes pusilla*, Walk., and I am able to confirm this name owing to the fact that some specimens collected by him in the Condobolin district of New South Wales in 1902 are in the British Museum; on the other hand, there are also specimens of his from the same district, but collected in 1899, and these belong to two species of *Austroicetes*, one being *A. tricolor*, Sjöst., while the other is undeterminable but clearly distinct from either *tricolor* or *pusilla*. As stated above, the species recorded by Newman as *Chortoicetes terminifera* represents some species of *Austroicetes*, similar to *tricolor*. Thus, there are two known species of *Austroicetes* which may be definitely considered as injurious and one more which cannot be identified at present, and there is little doubt that other species of this genus may take part in outbreaks.

Austroicetes pusilla, Walk. (Fig. 105).—Adult very small and slender. Head distinctly projecting above the pronotum; face in profile oblique, with frontal ridge shallowly sulcate; foveolæ of vertex impressed, elongate, narrowed forward. Pronotum constricted in front of the middle; median keel linear; lateral keels scarcely perceptible. Elytra reaching a little beyond the hind knees. Coloration brownish; pronotum with whitish X-shaped design and with pale lower hind portion of lateral lobes. Elytra with small brown spots along the middle. Wings hyaline. Hind femora with indefinite dark bands. Hind tibiæ pale yellowish. Length, male 14–15 mm., female 20 mm.; elytra, male 12–15 mm., female 18–19 mm.

FIG. 105.—Plain Grasshopper (after Rehn).

Austroicetes tricolor, Sjöst.—Adult somewhat larger than the preceding species and differing from it mainly in the frontal ridge not being sulcate, and the hind tibiæ red, with the base whitish, followed by a blackish ring.

Bionomics.—Froggatt (1903) records that females of these grasshoppers lay about 19 eggs on the average; while Newman, for the West Australian species, quotes 25–30 eggs as the average number; probably the difference is specific. The latter author states that there is only one generation a year, the eggs having an embryonic diapause lasting for 8½ months, and the hoppers hatching from the second week in July to mid-August, becoming adult in the middle of September or October. Eggs laid by the adults in November–December do not hatch even after warm autumn rains, but hibernate. In the more northern parts of Western Australia, the same author recorded two generations a year, but this may have been another species.

As regards their behaviour, Newman says that the hoppers in the first stage

are rather sedentary, but later regular wanderings of bands begin. The adults apparently migrate only when the swarms reach large dimensions; in New South Wales the swarms hatched in the interior may reach the coastal districts (Froggatt, 1903).

Newman points out the connection between the advent of agriculture and grasshopper outbreaks in Western Australia, but we will return to this question later.

The Larger Yellow-winged Grasshopper (*Gastrimargus musicus*, F.).

Adult (Fig. 106).—Of medium size, dark green or brown, with blackish markings. Pronotum well compressed from the sides, but very little constricted in the middle; median keel high, acute, in profile convex; hind angle acute; there is on the upper surface a white X-shaped mark, but it is seldom strongly developed. Elytra reaching well beyond the hind knees, with numerous blackish spots. Wings in the basal portion bright yellow, then with a broad black band, touching the hind margin of the wing; beyond the band hyaline. Hind tibiæ red. Length, male 28–30 mm., female 34–44 mm.; elytra, male 29–34 mm., female 33–41 mm.

Fig. 106.—Larger Yellow-winged Grasshopper, natural size (original).

Distribution.—This grasshopper has been incorrectly identified by Australian entomologists as *Locusta danica*, and its distribution has been, accordingly, described in the local literature as comprising nearly the whole of the Old World. Sjöstedt (1921) also confused it with *Gastrimargus marmoratus*, Thunb., and believed it to occur in India, Africa, etc. In fact, however, the Australian species is confined to that continent, but is known there from all States. Outbreaks of it are known in various places, notably in Queensland (Girault, 1913), Victoria, and New South Wales (Froggatt, 1910).

Bionomics.—Girault (*l.c.*) states that a female lays on the average 53 eggs (30–81). He observed oviposition only in the artificial soil of a railway bed, but this shows, in any case, that the species would normally oviposit in loose soils. In habits the hoppers were gregarious, and the adults undertook drifting flights, but not in dense swarms. Girault says that there was only one generation a year, but from his data it is clear that there were two generations, since adults observed in January gave rise to hoppers appearing towards the end of

February ; the hoppers became adult at the end of March ; oviposition took place in the middle of April, and eggs remained to hibernate.

THE SMALLER YELLOW-WINGED GRASSHOPPER (*Oedaleus australis*, Sauss.).

Adult Insect (Fig. 107).—Similar to the preceding species, but considerably smaller ; pronotum shorter, with the median keel low and the hind angle obtusely rounded ; black band of the hind wings not touching the hind margin. Length, male 20–22 mm., female 25–28 mm. ; elytra, male 17–23 mm., female 22–25 mm.

FIG. 107.—Smaller Yellow-winged Grasshopper, enlarged (original).

Distribution. — Sjöstedt confused this species with *O. senegalensis*, Kr., known from Africa and Western Asia, but it is in fact a local Australian species, though its distribution in Australia is still very imperfectly known, the available records referring only to Queensland and New South Wales. Froggatt (1907) says that during an outbreak in the latter State this grasshopper occurred mainly on hard open-grassed ridges.

Bionomics.—No exact information is available, except that the egg-pods are papery and contain 30–50 eggs each (Froggatt, 1907).

Economic Importance.—According to Froggatt (*l.c.*), this species may be very harmful during outbreaks, and it must be considered an important potential pest, with a tendency to swarm.

THE GRASSHOPPER AND LOCUST PROBLEM IN AUSTRALIA

While the above fragmentary observations present a fair summary of our knowledge of the locusts and grasshoppers in Australia, it would be a mistake to conclude that outbreaks there are very rare and unimportant or that the problem is of no economic interest. Indeed, even in the past there have been cases of most serious devastations of whole districts by locusts and grasshoppers. while there is every reason to agree with Froggatt, who from a very long local experience, said that " the time is rapidly approaching when Australia will have to deal with the locust question " (Froggatt, 1912).

The peculiarity of the Australian position with regard to the grasshopper problem is the relatively very small proportion of land under cultivation, this being mainly concentrated in the better watered coastal districts. Gradually, however, the agriculturist is pushing further inland, where general conditions for the breeding of grasshoppers, particularly of *Chortoicetes* and *Austroicetes*, connected with hard soils, are most favourable. Moreover, the advance of cultivation is connected with certain measures that seem to be practised without

any regard to the general well-being of the country. Thus, Newman (1924) demonstrated very clearly how in Western Australia, by the ring-barking of large areas of timber, vast stretches of open uncultivated country were artificially created, and they proved to supply ideal breeding grounds for grasshoppers. There is little doubt that similar conditions occur in other parts of the continent, and it would be absolutely necessary to study the ecology of all local species of grasshoppers likely to become injurious in order to define the possible influence of various agricultural methods on them. It must be never forgotten that a really serious outbreak of grasshoppers, to say nothing of true locusts, would be extremely difficult to deal with in the enormous continent of Australia with its scanty population. At present our knowledge even of definitely injurious species is quite inadequate, and serious attention must be paid to the problem before it is too late.

CHAPTER XVIII

MISCELLANEOUS GRASSHOPPERS AND SPECIES THAT SWARM OCCASIONALLY

The present chapter includes information on a number of species of Acrididæ, mainly of solitary habits (though some of them are able to swarm occasionally), that are injurious to different crops in tropical and subtropical countries. It has not been found convenient to discuss them with the solitary grasshoppers of temperate regions (see Chapter XVI), since the latter represent a more or less uniform biological and ecological group, while the species dealt with in this chapter nearly all differ widely in their habits, some of them being very specialised.

All species, known in the literature as injurious, are not included here, but only those that may be considered more or less regular, or very dangerous, potential pests. The number of species that have been recorded as injurious is very large, but a great many of the records are very doubtful, either as regards specific determinations or the economic importance of the species concerned. Indeed, it is a fairly common practice amongst economic entomologists to record as injurious almost every species found in sufficient numbers amongst crops, especially when there are traces of injury to plants.

In omitting many such species, I do not wish to imply that observations on species that are very occasionally injurious should not be made or recorded. On the contrary, there are several cases known when a species, not normally at all harmful and not even very numerous, has become suddenly both exceedingly abundant and very injurious, and it should be the duty of every economic entomologist to keep an eye on all possible pests. The point is, however, that practically any species of Acrididæ, except some few monophagous ones, may become a pest of some cultivated plant or other, especially in the tropics, where there is a great variety of the latter. To cover the whole ground, therefore, it would be necessary to give a systematic account of nearly all Acrididæ, and this is entirely beyond the scope of this work.

A very complete review of the species recorded in the literature as injurious has been given recently by Zacher (1926).

The Jola Grasshopper (*Colemania sphenarioides*, I. Bol.).

Adult Insect (Fig. 108).—Size, small (male) or medium (female). Body elongate, subcylindrical, in the male more or less strongly inflated in the middle. Head elongate, conical; fastigium of vertex seen from the side longer than the eye; frons strongly oblique. Pronotum conical, with feeble furrows and without

keels ; hind margin obtusely sinuate. Elytra rudimentary, very narrow, linear, longer than pronotum ; wings absent. Prosternum with an acute tubercle. Hind femora slender. General coloration greenish-yellow, or pale olivaceous ; head behind the eyes with a purplish stripe ; antennæ blue-black ; vertex with a bluish-black median stripe ; pronotum above reddish ; lateral lobes reddish above, black along the middle, their lower margin yellow ; elytra reddish, with the veins pale ; hind tibiæ reddish, at least apically. Length, male 23–40 mm., female 25–40 mm. ; elytra, male 6–9 mm., female 5–8 mm.

Hoppers.—In the earlier stages the colour of the hoppers is mainly greyish, mottled with brown, and a pale band runs along the head (beginning behind the eyes) and lower edge of the lateral pronotal lobes ; in later stages the colour gradually changes to greenish and yellowish, with blackish and red markings as in the adult. The stages differ mainly in the number of antennal joints (first, 8 ; second, 9–10 ; third, 10–12 ; fourth, 13–15 ; fifth, 15–17 ; sixth, 17–18), in the structure of the genitalia and in the size and position of the rudiments of wings and elytra (for details, see Coleman, 1911).

Fig. 108.—Jola Grasshopper, male, twice natural size (original).

Egg-pods.—The eggs are laid somewhat irregularly in vertical burrows ; they are only slightly cemented together, and the outer covering is also very fragile. The size of the egg-masses varies from 13–23 mm., while the number of eggs is, on the average, 38 (from 8–72) ; the eggs are arranged somewhat irregularly and in a vertical position.

Distribution and Ecology.—The Jola Grasshopper is a typically South Indian species, known mainly from the southern parts of the Bombay Presidency, from Mysore and Madras. The ecological data are scanty and refer exclusively to the secondary habitats of the species in cultivated fields, where it shows some not very definite preference for black soils, as opposed to red laterite soils ; this preference is, apparently, due to oviposition being easier in the black soils. The eggs are laid often at the bases of bushes, especially of *Cassia auriculata* or in cracks in the soil ; egg-laying on grassy patches seems to be less usual.

Bionomics.—The eggs hatch in July after the early monsoon rains, but the adult stage is reached only late in October and November, the hoppers passing through 5 or 6 stages (see p. 49). Pairing takes place soon after the adult stage is reached, and oviposition begins soon afterwards, continuing through November and December, but by the end of the latter month most of the insects

are dead. The eggs remain in the soil till the following monsoon season, *i.e.* there is a long embryonic diapause.

There are no data on the behaviour of the Jola Grasshopper, but it is stated to be somewhat sluggish and weak in its movements generally.

The chief damage is done to sorghum (*Andropogon sorghum*), locally called jola, but all other dry land cereals are also attacked, as well as certain leguminous crops (*Phaseolus mungo*, *Dolichos lablab*, *Cajanus indicus*) and, to a less degree, cotton.

Control.—Coleman recommends collecting hoppers by means of bags swept over the crop and deep ploughing against the eggs, the latter measure requiring experimental confirmation. Ballard and Muliyil (1921) applied poisoned baits with success (see p. 188).

The Spotted Grasshopper (*Aularches miliaris*, L.).

Adult Insect (Fig. 109).—A large and showy insect of rather clumsy general build. Head shining black (or yellowish or greenish-black); face often

Fig. 109.—Spotted Grasshopper, natural size (after Hutson).

yellow. Pronotum above with numerous large tubercles, wholly yellow, or with the central portion blackish; lateral lobes yellow. Elytra extending beyond the hind knees, greenish or olivaceous, with numerous round yellow spots. Wings purplish-brown basally, paler apically. Abdomen black, with reddish bands, or yellow markings. Length, male 40–50 mm., female 45–65 mm.; elytra, male 35–42 mm., female 35–55 mm.

Hoppers.—During the first four stages the hoppers are dark brown to blackish, with pale-yellow to orange-yellow markings arranged in longitudinal stripes. During the fifth stage, the rudiments of the elytra and wings become turned upwards and quite distinct. The sixth-stage hoppers resemble the adults in appearance and coloration except that the elytra and wings are not developed.

Egg-pod.—Outer cover porous, but firm. Shape cylindrical, straight or slightly curved. Length from 37 to 75 mm. Eggs 45 to 115 in number, pale yellow when freshly laid, but gradually darkening to reddish-brown or purplish before hatching.

Distribution and Ecology.—The Spotted grasshopper occurs all over India, ranging from Nepal and Sikkim to Ceylon and extending also into the Malay States and Java. In Ceylon, where the species is particularly important economically, it occurs mainly in the northern portion of the Central Province.

No proper ecological data on this species exist. Green (quoted by Hutson, 1926) says that the sites for oviposition appear to be selected quite at random, and the eggs are equally distributed in loose sand, stiff clayey soil, and ordinary loam ; these observations refer, however, to a mass outbreak when abnormal egg-laying may be expected. The hoppers and adult insects live on shrubs and trees.

Bionomics.—The adults appear in Ceylon late in July and become sexually mature three or four weeks later, *i.e.* about the end of August. During the next three months, the insects continue feeding and mating at irregular intervals, but become gradually more sluggish. About the middle of November, the mating pairs assemble together in vast numbers, and oviposition begins ; this seems to indicate that pairings previous to this are probably only trial ones and that the females, at any rate, do not become sexually mature until late. The eggs are laid during the last half of November. On the whole, the adult period occupies about $4\frac{1}{2}$ to $5\frac{1}{2}$ months, and it may be assumed that most of it is passed in the imaginal diapause. The eggs hatch after a diapause of about 4 months coinciding with the dry period. The development of the hoppers occupies from $4\frac{1}{2}$ to $5\frac{1}{2}$ months, so that the whole cycle takes from 13–15 months ; this figure seems somewhat doubtful, and is probably due to the abnormally long period of larval development in cages as observed by Hutson ; normally, it must be a full year.

As regards behaviour, the young hoppers cluster on weeds and low-growing shrubs, but older ones are more active and apparently move about. The winged adults are very active, flying from one tree to another and can spread over a large area ; apparently, no flights in swarms or groups are known.

Economic Importance and Control.—The spotted grasshopper in Ceylon is a fairly regular pest of various plants, particularly of dadap (*Erythrina lithosperma*), coconut, areca nut, etc.

Control measures usually recommended are based on collecting the insects, which can be done most easily during oviposition and in the first hopper stages. There is little doubt that the hoppers can be controlled by poison baits, but no experiments in this direction have ever been made.

For further information on the species, see Hutson, 1926, on whose paper the above account is based.

THE ELEGANT AND THE VARIEGATED GRASSHOPPERS (*Zonocerus elegans*, Thunb., and *Z. variegatus*, L.).

Adult of the Elegant Grasshopper (Fig. 111).—Of medium size, rather clumsy, brilliantly coloured. Antennæ black, with the apex and several rings orange. Head above black, sometimes with yellowish lines and small spots, but the black colour predominates ; face and sides of the head black, with yellow stripes and small knobs. Pronotum conical, without any keels,

yellowish-olivaceous, paler at margins. Elytra covering about two abdominal segments (or fully developed), pale olivaceous or pinkish-black at the base; wings absent (or fully developed and then pinkish, smoky towards the apex). Abdomen yellowish-olivaceous, the base of each segment black. Legs

FIG. 110.—Variegated Grasshopper, twice natural size (original).

variegated with black, yellow, and red. Hind femora olivaceous; outer face near the apex black. Length, male 28–36 mm., female 35–50 mm.; elytra, male 5–9 (or 29–35) mm., female 10–12 (or 27–31) mm.

Adult of the Variegated Grasshopper (Fig. 110).—Very similar to the preceding, but the head above mainly yellow with reduced black pattern; antennæ with only 1–2 yellow rings; elytra practically always developed, green, without pink colour; wings developed, decidedly smoky; legs more gaudily variegated in black, red, and yellow; hind femora mostly black, with a yellow ring before the knees; abdomen with black spots not rings. Measurements as in the other species.

FIG. 111.—Elegant Grasshopper; above, an adult of the brachypterous form, natural size; below, a hopper, enlarged (both original).

Hoppers of the Elegant Grasshopper (Fig. 111).—Strikingly coloured in black and white (or yellowish). Antennæ black with white tips. Face with white spots. A narrow white line runs along the back, and it is included between two broader black stripes; sides with a broad white stripe and, below, a black one.

Front and median legs with white spots; hind legs with white marginal lines.

Hoppers of the Variegated Grasshopper.—These have never been described, and their points of difference from those of the other species are not known, but in general appearance they must be very similar.

Egg-pods of the Elegant Grasshopper.—Outer covering brittle; length about 25 mm., diameter 6–9 mm. Eggs yellow just after being laid, but turn brown later; their number varies from 23 to 116; length about 6 mm., diameter 1·5 mm.

Distribution and Ecology.—Both species seem to be distributed all over Tropical and South Africa, but the Elegant Grasshopper is apparently more at home in South Africa, where it replaces the other species entirely, while the latter occurs alone in the more northern areas (Senegal, Nigeria, etc.); the exact areas of distribution of both species are, however, not sufficiently known, partly owing to the fact that they are very often confused.

Ecological data are practically lacking. In South Africa the Elegant Grasshopper prefers more humid parts, such as the Natal Coast and Zululand (van der Merwe and Kent, 1925; the paper of these authors is the main source of information on the species). Both species are phytophilous in habits, climbing various low-growing shrubs.

Bionomics.—The Elegant Grasshopper in South Africa hatches from the end of September to the end of October, the hatching usually taking place after rains. Young hoppers congregate in dense clusters on the tips of plants, but scatter later. The adult stage is reached 73–78 days after hatching, but the number of larval stages is not known. The adults sometimes congregate in large numbers, but do not form really dense swarms and do not wander together, except for short distances. Even the individuals with fully developed wings, which occur occasionally, are very poor fliers. Pairing takes place soon after the adult stage is reached, and as the eggs are laid about four weeks later, it may be presumed that there is a short imaginal diapause. Oviposition occurs from February to May, so that the eggs remain in the ground for about six months, there being only one generation a year (van der Merwe and Kent). The dates of appearance of the stages in East Africa differ but little, the hoppers hatching in October; in January the adults appear, and they disappear after oviposition in May (Zacher, 1926).

The annual cycle of the Variegated Grasshopper in French Equatorial Africa is similar, there being also only one annual generation; the hoppers hatch in the middle of February and in March; the adults pair in September–October (Vayssière and Mimeur, 1925).

South African observations show that the Elegant Grasshopper has some preferences among wild food plants, such as a milkweed, *Asclepias fruticosa*, and species of *Senecio*. Apart from these, however, a large number of very different plants are subject to attacks, including almost any cultivated plants, though grasses are not touched.

Economic Importance and Control.—Both species being practically omnivorous and occurring often in very large numbers, a great deal of damage is done to various crops, particularly to cotton, cacao, coffee, rubber,

camphor, etc. Since, however, the grasshoppers feed also on various weeds, the damage they do is not so serious as it might otherwise be ; it may be suggested that they would be more dangerous to very clean crops that are free from weeds.

As regards control, these grasshoppers are so sluggish that there is little danger of them spreading over large areas ; accordingly, they must be regarded as pests of very localised importance and control measures may be taken individually by farmers, there being hardly any need even for co-operative efforts, though these might be more effective. From the technical point of view, spraying with any internal poison may be recommended, while contact insecticides may be also used with success against younger hoppers clustered on plants. Van der Merwe and Kent, after making some experiments with baits of *Senecio* dipped in poison, came to the conclusion that there is little hope of finding baits that would be more attractive than natural fresh food ; this conclusion can hardly be drawn from the very few and imperfect experiments made, and further attempts in the same direction would be desirable. It may be worth while studying the chemical properties of *Senecio*, *Asclepias*, and other favourite food plants, in order to discover the attractive substance. In East Africa baits of horse dung, sugar, and salt have been used with success (Zacher, 1926).

The Larger Rice Grasshoppers (*Hieroglyphus* spp.).

Species of this genus has been often recorded in the literature as pests of rice and some other crops, but nearly always only one species, *H. banian*, F. (*furcifer*, Serv.), has been regarded as a pest, owing to the confusion in the systematics of the genus. A recent revision (Uvarov, 1922) has enabled me to clear up the synonymy of the species and to establish the fact that the species most often injurious in India is actually *H. banian*, but that some other species of the genus also occur together with it, or separately, as real pests. Since, however, the bionomics only of *H. banian* have been studied sufficiently (Coleman and Kuhni Kannan, 1911), I will only discuss that species in detail. Economic entomologists should be careful to pay close attention to the exact determination of such species, since details of their bionomics may be different in spite of their great superficial likeness.

Hieroglyphus banian, F. (Fig. 112).—Adult of medium size ; uniformly pale green ; antennæ brownish, with narrow pale rings ; pronotum with the transverse furrows black ; hind tibiæ bluish. Face oblique. Pronotum round, with faint traces of a median keel, but without lateral keels ; transverse furrows deep. Prosternum between the bases of front legs with a straight conical spine. Elytra and wings fully developed. Hind tibiæ rounded, not expanded. Male cerci bifurcate at the apex (Fig. 113, B). Female ovipositor with blunt teeth. Length, male 28–34 mm., female 34–44 mm. ; elytra, male 20–27 mm., female 24–34 mm.

Hoppers.—In the first stage the ground colour of the body is yellowish, but with numerous reddish-brown spots and patches ; along the middle of the back there runs a bright greenish-yellow stripe, about $\frac{1}{2}$ mm. broad, included

between two dark brown bands. In the second and third stage, the colour remains more or less the same, but from the fourth stage onwards, the hoppers present variations in colour, some retaining the same type as before, others becoming almost uniformly green, while still others become very dark, the sublateral stripes on the back and face assuming a black shade. The stages can be separated by the number of antennal joints (see p. 45) and by differences in the structure of the genitalia and the rudiments of the wings and elytra (for details, see Coleman and Kuhni Kannan, *l.c.*).

Egg-pod.—Very firm and tough, so much so that it is difficult to get the eggs out of it. The upper part represents a spongy stopper 9–15 mm. in length. The eggs average 39 in number (7–59), arranged in rows, but are not very regular; they are yellowish; average length $5\frac{1}{4}$ mm., diameter $1\frac{1}{4}$ mm.

Distribution and Ecology.—*H. banian* seems to be the commonest species of the genus in India and is distributed all over the plains, though the northern limits of its area are as yet not known; it does not seem to range into Assam.

Fig. 112.—Larger Rice Grasshopper, *Hieroglyphus banian*, F., ♀, natural size (original).

While the hoppers and adult insects are usually observed in rice-fields, oviposition takes place in grassy places near them, not in the fields themselves.

Bionomics.—Eggs are laid in the South of India during October to December, and remain in the embryonic diapause until the following June or July. The hoppers on hatching grow quite rapidly and pass through six or seven stages (see p. 49), the adults appearing from the middle of September to November. The hoppers and adults move little; the latter, though provided with wings, fly only when disturbed.

The food plants of *H. banian* mainly comprise Graminaceous plants, both wild and cultivated, those most attacked being rice and sugar-cane, though *Sorghum*, millet, *Setaria*, etc., are often seriously damaged. Other recorded food plants include *Phaseolus aconitifolius*, *Sesamum indicum*, and others, but these data may refer to other species of the genus.

Control.—Coleman and Kuhni Kannan (*l.c.*) came to the conclusion that the best method of controlling this pest is to collect the hoppers by means of large bags drawn quickly over the grass where they have hatched. They found ploughing against the eggs ineffective, while spraying they also considered unsatisfactory. It should be stated, however, that baits were not tried, except those of cut grass, while the results of the spraying experiments were not convincing.

Other Species of Hieroglyphus.—Probably, next in importance to

H. banian in India comes *H. nigrorepletus*, I. Bol. This is a larger insect, with the pronotum somewhat flattened above and very heavily marked with black in the transverse furrows on the lateral lobes; the male cerci are obliquely truncate at the apex, not bifurcate (Fig. 113, N); the elytra may be either abbreviated or fully developed; the size varies as follows: length, male 30–42 mm., female 38–48 mm.; elytra, male 12–16 (or 31–37) mm., female 10–16 (or 39) mm. In its distribution *H. nigrorepletus* seems a more southern insect than *H. banian*, occurring all over the Indian Peninsula, but hardly spreading further north than Allahabad and Pusa. The bionomics and even economic importance of *H. nigrorepletus* cannot be very definitely established owing to the confusion of records; it does not seem to be a very serious pest of rice, and it is probably more closely connected with the crops growing under less moist conditions such as *Setaria* and *Andropogon*.

Another Indian species recorded as a pest of rice is *H. oryzivorus*, Carl., which may be recognised by its saddle-shaped pronotum and by the male cerci being provided with a conical appendage on the inside of the apex (Fig. 113, O). It is known from several localities in the Indian plains and has been reported as damaging rice in the Central Provinces.

H. concolor, Walk., is the fourth Indian species which may be injurious to crops, but the records of it are vague.

H. annulicornis, Shir., a large species with the cerci simple (Fig. 113, A), has been recorded by Matsumura (1910) as a pest of sugar-cane and of *Canna indica* in Formosa; it also occurs in India, but its economic status there is unknown.

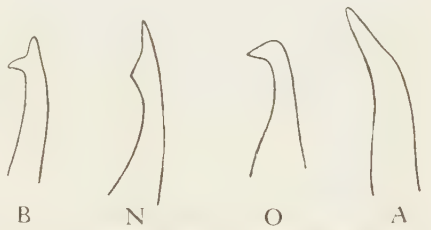

Fig. 113.—Male cerci of different species of Larger Rice Grasshoppers: B, *Hieroglyphus banian*; N, *H. nigrorepletus*; O, *H. oryzivorus*; A, *H. annulicornis* (original).

Two species of the genus are known from Africa (*H. daganensis*, Kr., and *H. africanus*, Uv.), but there are no records of their being injurious.

The Smaller Rice Grasshoppers (*Oxya* spp.).

The Species involved.—Records of injurious species of *Oxya* in the literature practically all mention one species, *O. velox*, F., but this is merely due to the fact that until recently there was no revision of species of this difficult genus, and the majority of records are, therefore, not referable to any particular species. The revision published recently by Willemse (1925; see also Uvarov, 1926*a*, where some important synonymic corrections are given) comprises as many as 30 different species, several of them being recorded definitely as pests, while many others are probably so. Those that are known to be injurious are as follows:

O. intricata, St. (*O. universalis*, Will., *O. insularis*, Will.).—A widely distributed species, ranging from Formosa, China, Malay Peninsula (very common in rice-fields), Siam, Ceylon, Bombay (doubtful record) to Sumatra, Celebes, Philippines, Carolines, and Moluccas.

O. fuscovittata, Marsch. (*O. turanica*, Uv.).—Baltistan in India; Russian Turkestan (injurious to rice, Plotnikov, 1926).

O. bidentata, Will.—Peshawar, N.W. India (injurious to sugar-cane).

O. oryzivora, Will.—India (on rice).

O. uvarovi, Will.—Peshawar, Punjab, Bengal (on sugar-cane).

O. multidentata, Will.—Widely distributed in the plains of India (sugar-cane).

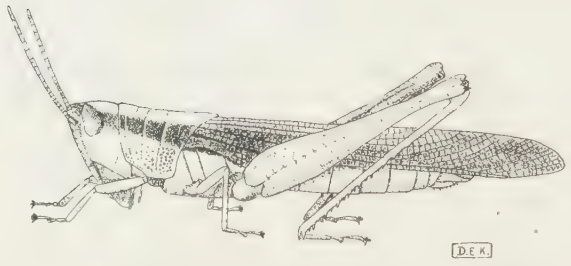

FIG. 114.—Smaller Rice Grasshopper, *Oxya multidentata*, Will., ♀, enlarged (original).

O. chinensis, Thunb. (*sinensis*, Walk.).—A very widely distributed species occurring in Japan, China, Ceylon, Cambodia, Siam, Burma, Federated Malay States (common in rice-fields), Sumatra, Java, Lombok, Borneo, Celebes, Moluccas, Philippines, New Pomerania, Hawaiian Islands (pest of sugar-cane, recorded as *O. velox* by Muir and Swezey, 1927), Queensland, and Mauritius.

O. hyla, Serv. (*viridivitta*, Walk.).—All over Africa, south of the Sahara; Madagascar (in rice-fields, according to a communication from B. N. Zolotarevsky).

All these species, as well as the majority of the others known in the genus,

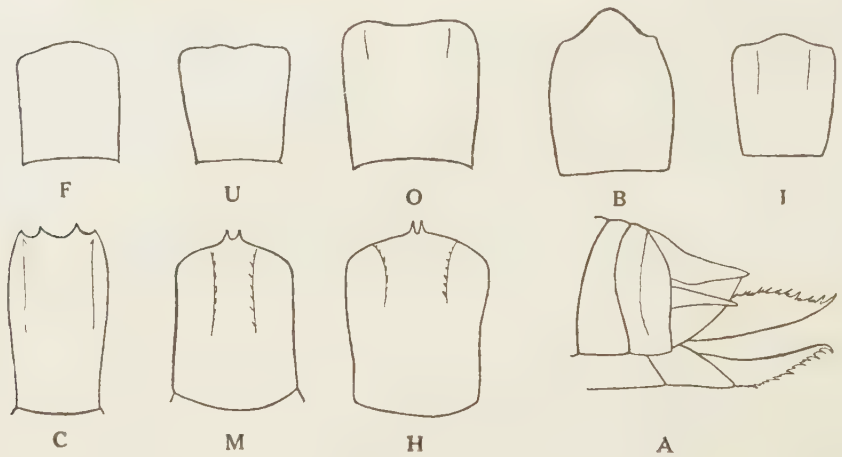

FIG. 115.—Female subgenital plates of different species of *Oxya*: I, *intricata*; F, *fuscovittata*; B, *bidentata*; O, *oryzivora*; U, *uvarovi*; M, *multidentata*; C, *chinensis*; H, *hyla*; A, ovipositor of *O. intricata* (after Willemse).

are exceedingly similar to each other in their general appearance and in the type of coloration, the specific differences being mainly in the structure of the female subgenital plate and the ovipositor. I will give only a brief general description of the genus, while a figure (Fig. 115) may help to determine tentatively some of the species known as pests.

Adult Insect (Fig. 114).—Of medium size or small, rather slender, shining green or yellowish, with a sharp black lateral stripe (sometimes faint or absent).

Face in profile oblique ; frontal ridge distinctly furrowed. Antennæ slender. Pronotum round, with the disc somewhat flattened ; no lateral keels ; median keel slightly perceptible in the hind portion of the disc. Prosternum with a cylindrical spine. Elytra fully developed (in some species abbreviated) ; their front margin expanded near the base. Hind tibiæ usually bluish with their margins somewhat expanded, very acute. First joint of the hind tarsi expanded.

Bionomics.—Apparently all species of *Oxya* are confined in their habitat to marshy places. The species occurring in the Hawaiian islands, *O. chinensis*, is connected in its distribution with the nut grass (*Cyperus*), and damages sugar-cane fields only where there are patches of *Cyperus* adjoining them. The insect can also live in grasses and rice-fields covered by water, and it can swim with the help of its hind legs, which are specially adapted for the purpose (expanded tibiæ and tarsi). In India these grasshoppers are stated (Ramachandra Rao, 1921) to breed throughout the year, but are more numerous in the rainy season from August to November. The eggs are laid in different ways, according to the conditions ; in dry weather they are laid in the soil ; but if the field is flooded, they may be laid between rice stems or grass clumps an inch or two above the level of the water. The number of eggs in an egg-mass varies from 10–29. Hatching occurs within 15–41 days, depending on the weather conditions. There are six larval stages, but the females sometimes have an additional stage ; the adult stage is reached in the Hawaiian species (from observations in captivity) after 6–10 weeks, and it is theoretically concluded that two broods a year are possible. Two annual generations are recorded also for a species of *Oxya* in Formosa (Sonan and Fukuda, 1926).

The chief damage done by these grasshoppers is in the rice-fields, where they cause the ears to wither by biting them at their base when they are maturing. They also damage the leaves of sugar-cane (Hawaii, India), and, occasionally, cotton and pulses in India.

Control measures have not been worked out, but it would seem that some kind of poison baits may be found, while spraying of wild marsh grasses, amongst which the insects breed, may be also tried. Ramachandra Rao (*l.c.*) recommends catching the grasshoppers with bags, but this would seem a very laborious and not very effective procedure.

The Tree Locust (*Anacridium moestum*, Serv.).

Adult Insect (Fig. 116).—Very large, but rather slenderly built. Antennæ long, black. Head, thorax, and abdomen reddish-brown, or grey, indefinitely mottled with paler and darker colour. Face in profile slightly oblique ; frontal ridge above the median ocellus dilated and flat, below it furrowed. Pronotum convex, punctured ; median keel raised, thick, in profile feebly convex, deeply cut by transverse furrows. Prosternal spine compressed laterally, slightly bent backwards. Elytra extending to the apex of the hind tibiæ, grey, with blackish streaks on some of the veins. Wings long and narrow, hyaline, with a broad black band near the base (in the more northern form, subsp. *melanorhodon*, Walk., the band is not sharply defined, incomplete, and not black, but

smoky), and a few black small spots near the apex. Hind femora with blackish bands above. Hind tibiæ purple; their spines whitish basally, red in the middle and black apically. Subgenital plate of the male trilobate apically, the middle lobe being shorter than the lateral ones; male cerci long, slender, incurved. Length, male 50–55 mm., female 56–65 mm.; elytra, male 58–62 mm., female 60–74 mm.

Hoppers.—No exact description of the various stages exists, but Johnston (1924, whose paper is practically the only source of information on this species, and my account is based on it) says that the young hoppers are yellowish-green with yellow antennæ; in the later stages, two types of coloration are

Fig. 116.—Tree Locust, ♂, natural size (original).

noticeable, some amongst them being uniformly light green, while the others have numerous black spots and markings on the body and legs and the veins of the wing rudiments are also dark; the ground colour of the second form may be either green or yellow. (Adults bred from the two forms appear to differ very markedly in size, the green hoppers producing larger individuals.)

Egg-pod.—About 75 mm. in length, containing 150–200 eggs. The latter are first yellow, but soon change to a brown colour.

Distribution and Ecology.—The typical form of the species (*moestum*) is distributed all over South and East Africa, ranging northward up to North Uganda and Northern Nigeria, while the subsp. *melanorhodon* represents a more northern race, known from the Sudan, Sokotra, Abyssinia, Arabia, and Cape Verde Islands.

Thus, nearly the whole of Africa seems to be inhabited by this species, with

the exception of the forest regions of Central and West Africa, into which it does not seem to penetrate, being intimately associated in its distribution with the savannahs with scattered *Acacia* trees. Both hoppers and adults are strongly phytophilous in their habits, living always on trees or bushes.

Bionomics.—The life history in the Sudan seems to be as follows. Pairing and oviposition take place in summer during the rains, the eggs being laid only after the ground has become moist. The eggs hatch in about six weeks, and the hoppers immediately climb the nearest trees or shrubs, which they do not leave unless in search for fresh food. After passing through five stages, which takes about a month, the hoppers become adult. The latter stage has a very prolonged imaginal diapause since sexual maturity is not reached until the next June ; the insects live all that time in the trees, in small swarms or singly, and seem to undertake short flights, particularly at night, when they are often attracted by light.

The favourite food appears to be leaves of various species of *Acacia*, but *Zizyphus* trees are often preferred to them. Other trees, such as *Capparis aphylla* and gum trees, are also subject to attack, but of cultivated crops only occasional damage has been reported to cotton in the Sudan. In South Africa fruit trees have been damaged (Lounsbury, 1924).

Economic Importance.—It would appear from the above that the economic importance of the Tree Locust is very slight, and the reason for including it in this book is the fact that it undoubtedly was, and still is, very often confused with the Desert Locust, which it resembles superficially. Vayssière and Mimeur state that some of the records of swarms of the Desert Locust in French Equatorial Africa proved on examination of specimens to refer to the Tree Locust, and there is little doubt that the same thing has often happened in other parts of Africa also. The differences between the Tree Locust and the Desert Locust are well marked and easily seen. In the first place, the black, or at least dusky, band of the hind wings is very characteristic of the Tree Locust, while in the Desert Locust the wings are absolutely without any markings. Further, the male subgenital plate of the Desert Locust is bilobate, while that of the Tree Locust is trilobate ; the male cerci of the Desert Locust are short, broad, flattened, and truncate apically, while in the Tree Locust they are slender, round, and curved. The hind tibiæ of the Desert Locust are yellowish, and those of the Tree Locust are conspicuously marked (see above).

It is also not impossible that some of the records of damage by the Desert Locust should really apply to the Tree Locust, which, as we know definitely, is able to form small swarms and attack at least fruit trees. Johnston says that in the winter of 1923 native orchards along the river near Khartoum were invaded, and many trees, particularly limes, were defoliated.

The Bombay Locust (*Patanga succincta*, L.).

Adult Insect (Fig. 117).—Large, rather slender. General coloration pale brown (red or reddish in migrating individuals, dark brown during the oviposition period), with streaks of black and yellowish. Pronotum distinctly com-

pressed laterally and somewhat constricted in front of the middle ; median keel very low, almost obliterated, owing to the coarse honeycombed sculpturation of the upper surface of the pronotum ; lateral keels absent ; upper surface dark, with a pale stripe along the median keel ; lateral lobes with a black stripe above the middle and a large yellowish spot in the middle, otherwise dark. Prosternal spine inclined backward, not touching the mesosternum, acute. Elytra extending well beyond the hind knees, mainly pale, with ivory-white stripes and black spots along the middle, and black narrow streaks in the apical part. Wings rose at the base. Hind femora pale, without bands. Hind tibiæ pale. Length, male 48–56 mm., female 57–63 mm. ; elytra, male 55–59 mm., female 58–70 mm.

Hopper of the First Stage (descriptions after Lefroy, 1906, on which paper the article is entirely based).—Green, with tiny black dots visible only under a lens. Antennæ yellow. Length 7 mm.

Hopper of the Second Stage.—Antennæ slightly brown. Dark speckling more abundant and distinct. A dark line on each side of the median dorsal line, which is pale. Length 11 mm.

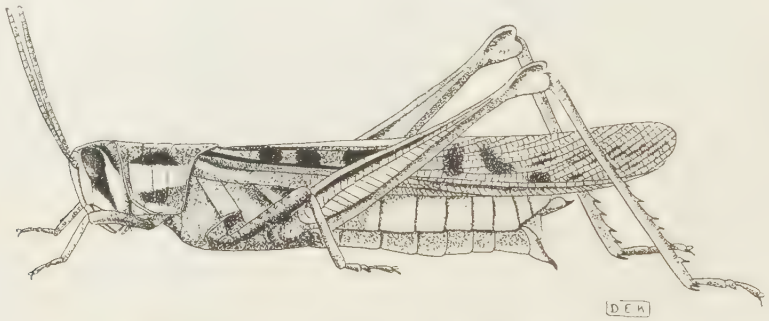

Fig. 117.—Bombay Locust, ♀, natural size (original).

Hopper of the Third Stage.—Antennæ dark-brown, 16-jointed. Median dorsal line white with a broader dark line on each side. Length 13 mm.

Hopper of the Fourth Stage.—Antennæ black, white ringed, 21-jointed. General colour green, with very distinct black speckles and a double dorsal stripe. Rudiments of wings and elytra green. Length 15 mm.

Hopper of the Fifth Stage.—Antennæ black, white rings fainter, 22-jointed. General colour green, slightly yellowish above ; stripes and speckles very distinct ; dorsal stripe without the inner pale line. Length 23 mm.

Hopper of the Sixth Stage.—Antennæ as before, 23-jointed. General colour light green, with the dorsal black line. Speckles on pronotum turning brown. Rudiments of elytra and wings with two black spots each. Length 30 mm.

Hopper of the Seventh Stage.—General colour light green, with a brownish tinge all over ; legs reddish-brown. Wing rudiments 14 mm. long.

Egg-pods.—Straight or curved according to the nature of the soil, 25–50 mm. long. Outer cover fragile, and the egg-pod can only be taken out of the soil soon after oviposition ; later it becomes impossible to do so without breaking it. Eggs yellow, about 8 mm. long, their number 110–120.

Distribution and Ecology.—This species is distributed all over Southern and South-Eastern Asia and the Malayan Archipelago, but its exact range is as yet incompletely known. According to Fletcher (Proc. Third Entom. Meeting, Pusa, i, p. 310), it " occurs throughout the plains of India and Ceylon," but its northern and western limits are not known. Lefroy believes that a permanent breeding region exists in the forests of Kanara, Goa, and neighbouring districts.

Ecologically the species seems to be associated with forests in the adult stage, but oviposition takes place in more open grassland, amongst scrub, or on the edges of cultivated fields, but always in more or less open spaces, and the hoppers live there. The soil selected for oviposition is neither too dry nor waterlogged ; a softer, less tenacious black soil is preferred to a stiff reddish clay.

Bionomics.—The annual life cycle of the Bombay Locust is characterised by the very long period of the imaginal diapause, which permits of only one generation a year.

The eggs are laid in Western India in June and July, and the hoppers emerge in six weeks, on the average, though the incubation period may occupy up to eight weeks. The number of hopper stages has been found to vary (in captivity) from seven to nine (in one case), the total time of development occupying 61–71 days.

The hoppers, even when very abundant, do not form bands and do not wander in masses. They live in grass, feeding on it and other vegetation, but the wild food plants have not been studied.

The adults congregate into swarms, if sufficiently abundant, and move towards cultivated areas, doing a good deal of damage. Their food at this period consists of sorghum (*Andropogon sorghum*), various millets (*Pennisetum typhoideum* and others), mango, citrus, coconut palms, *Eleusine coracana*, and a large number of forest trees. Cotton is not eaten.

Soon after the swarms begin, more or less definite migrations occur, mostly at night, this period occupying October and November and resulting in the swarms entering forests, where they remain in a very inactive state, apparently not feeding very much. While migrating, the general colour of the insects becomes red, so that a swarm settling on trees may be seen from afar. This colour changes to brownish with the commencement of the breeding period, which is preceded by a second migration, from the end of March to the end of May. After this, the swarms scatter, and pairing and oviposition take place during June to August.

These data are based on observations during one invasion of 1903, and it would not be safe to generalise from them. Indeed, it is quite possible that the annual cycle in normal years when the species is not swarming may be materially different.

Economic Importance and Control.—While this locust is a very common insect in India, mass outbreaks of it are very rare, the reasons for this being quite obscure. During outbreaks, however, it can do a great deal of damage to various crops. Its control is very difficult, because the eggs are not laid

by dense swarms, but by scattered females, and the hoppers, which might have been the easiest stage to control, are also scattered and concealed in grass. It is only when the adults appear and swarms are formed that the damage becomes serious and control is required, but the difficulties of organising it then on a sufficiently large scale are obvious. In any case the spraying of cultivated plants threatened by these locusts must be of value, while there is little doubt that an effective bait may be also found for them.

When it comes to organising a proper campaign against the Bombay Locust, the usual method of basing it on full and exact survey of breeding grounds of hoppers should be applied ; though difficult in this case, it is not absolutely impossible. Measures of some kind (perhaps dusting from aeroplanes) might be applied against hibernating adult swarms in forests, this stage stretching over a very long period.

The Javanese Grasshopper (*Valanga nigricornis melanocornis*, Serv.).

Adult Insect (Fig. 118).—Large, almost uniformly brown ; sometimes with a pale-yellowish, or yellowish-green stripe along the middle of the pronotum

Fig. 118.—Javanese Grasshopper, ♂, natural size, (original).

and the anal area of the elytra. Antennæ long, fine, blackish. Pronotum with large, but very shallow, almost obsolete, pits ; median keel somewhat raised, rather acute, slightly convex in profile. Prosternal tubercle compressed laterally, slightly inclined and bent backwards, but not touching the mesosternum. Elytra extending beyond the hind knees, not densely reticulated, semi-transparent even in the basal half, with some very faint blackish spots. Wings faintly reddish at the base, slightly smoky in the rest. Hind femora with indistinct dark bands. Hind tibiæ blackish-red all round, spines yellowish, with black tips. Male cerci flattened laterally, somewhat recurved at the apex, which is attenuate. Male subgenital plate acute. Length, male 46–50 mm., female 51–60 mm. ; elytra, male 45–51 mm., female 48–61 mm.

Hoppers not described in any detail.

Egg-pod.—Containing 55–114 eggs (average 71).

Distribution and Ecology.—*Valanga nigricornis*, Burm., is widely distributed, ranging from Indo-Malaya to Australia, but it is split up into a large number of local races (subspecies), and the subsp. *melanocornis*, Serv., is confined to Java. There it occurs chiefly in the teak forests of Middle Java, which

cover an area of about 2000 sq. miles and are situated about 200-300 feet above sea-level (Roepke, 1915, on whose work this account is chiefly based). These forests may be regarded as primary breeding areas of the insect, but during outbreaks, secondary ones may develop outside the forests, mainly in cultivated localities and at various altitudes up to 2700 feet above the sea.

In habits the Javanese grasshopper is decidedly phytophilous.

Bionomics.—The eggs are laid in any kind of soil about the period of the western monsoon. If the weather following oviposition is not too dry, the eggs may hatch in a few weeks, but drought may delay hatching until the November–December rains.

The strongly phytophilous habits of the hoppers and adults, together with their positive phototropism, cause them to congregate mainly on the tree-tops, which, consequently, suffer most damage. Favourite food plants are *Castilloa*, bread-fruit trees, *Ficus*, *Hevea*, coconut palms; Graminaceous plants are avoided, though maize sometimes suffers seriously. Plants immune from attack are mahogany trees, rice, lalang grass (*Imperata arundinacea*), *Saccharum spontaneum*, and *Coleus tuberosus*.

The adults sometimes change their locality, mainly from lack of food, but otherwise they are not migratory, and flights are not undertaken in swarms.

Roepke suggests that the probable cause of periodic appearances are a succession of abnormally dry monsoons, which delay the hatching of eggs so that hoppers appear simultaneously in large numbers. This view is, however, largely theoretical and is not based on direct evidence.

Economic Importance and Control.—In years of mass outbreaks which occur at long intervals, this grasshopper may cause very serious damage, but only in limited areas; the damage is particularly serious in the vicinity of secondary breeding places, which are often amongst crops. Control is very difficult owing to its arboreal habits, but poison may be used with success.

CHAPTER XIX

GENERAL CONCLUSIONS

On completing this book it would be useful to summarise very briefly the main results and, at the same time, to point out the direction of further work on the locust and grasshopper problem in general.

We have seen that the purely practical problem of locust and grasshopper control is most intimately connected with a detailed study of the insects themselves. Taking, for example, the present most widely used method of poison baits, it is clear that the success of its application depends on a thorough knowledge of the chemotropism of the species concerned, but we are unable to go far in our studies of this, since we do not even know for certain whether there are any organs of chemical appreciation in the Acrididæ, to say nothing of the details of their functions. Any studies in the anatomy, histology, and physiology of the sense organs are therefore urgently needed for purely practical purposes. The application of any other method of control similarly depends on a good knowledge of various points in the bionomics and behaviour of the insects. At the same time, it will be clear from the preceding chapters that our theoretical knowledge of the Acrididæ, though it has made some progress during the last two decades, is still amazingly inadequate. Though locusts and grasshoppers damage our crops, how little do we know of their nutrition, even from the point of view of their food plants, time and conditions of feeding, etc., let alone their physiology. Again, though we control locusts and grasshoppers by poison baits, we know nothing as to why and how the baits act on the insects. We poison the insects, but what do we know of the action of poisons on them? Absolutely nothing except what we have found empirically without understanding the essence of the process. We have before our eyes examples of swarming phases of several locusts, if not dying out, at least retreating, but what do we know about this all-important phenomenon, on which the whole future policy of control should be based? Again, absolutely nothing.

All these are large problems of general importance, but it is sufficient to glance at the multitude of details, from which our knowledge of each species is composed, to see at once that all the information is of a most fragmentary character. Indeed, fairly satisfactory, but still very far from complete, monographs are available for two species only (the Rocky Mountain Locust and the Migratory Locust), while on all other species, including the most important economically, nothing but disconnected fragments of information are available, and these are very often unreliable. Even our knowledge of the systematics of many species is most unsatisfactory, particularly in respect of the South

American and Australian species. When the species doing damage in a certain country is known, the degree of its economic importance, its distribution, ecology, and bionomics have never been studied in any detail. Even the purely descriptive side is exceedingly poor, since for the majority of economically important species there are no exact descriptions of all stages of development, though knowledge on these points is absolutely necessary for other studies and for practical purposes. Special emphasis must be laid on our deep ignorance of the problems of ecology of the ACRIDIDÆ, since it must be clear from this book that without a thorough understanding of the inter-relations between the insects and their environment, real progress in their control is impossible.

The results of this limitation of our knowledge are obvious. It is true that good progress has been made in the past in the study of the technical methods of control, and this still continues, but this has been, and still is, purely empirical. The time-honoured method of trial and error has been very costly to agriculturists, who have had to pay with their crops for all the experiments. The plans for the future solution of the locust and grasshopper problem itself, as opposed to that of separate outbreaks, are completely obscure, and only generalised suggestions can be made ; the problem can be approached only on the basis of the ecological method, which demands, first of all, an exact quantitative knowledge of all the conditions, and this is at present beyond any practical possibility.

What are the reasons for such a low level of our knowledge on ACRIDIDÆ ? The main one is clear. All that has been done so far towards the study of the ACRIDIDÆ in all countries is the result of the work either of casual investigators, partly unofficial and voluntary, or of temporary organisations, while special permanent laboratories for the thorough study of locusts and grasshoppers have never existed anywhere, except on paper.

This situation is due to the periodicity of damage done by ACRIDIDÆ. As soon as a large invasion begins, the question of the necessity of organising studies arises, but in many cases the invasion is over before any practical steps in that direction are taken ; when the danger is over, the problem is soon forgotten, and the proposed investigations never materialise. I have repeatedly drawn the attention of the reader to the fact that the periods of minimum are the very times when many problems of locust biology can be investigated most profitably and with definite practical results; in practice, in the intervals between outbreaks locusts disappear from the horizon of the economic entomologist, who is entirely occupied with other current work—until the next outbreak, which will unavoidably be " unexpected."

Thus, the main fault is in the lack of permanency in the studies on locusts and grasshoppers. This is being realised in some countries, but attempts to remedy the situation are both few and clearly inadequate, since a small laboratory, with one or two scientific workers without special qualifications, would be clearly unable to obtain really valuable results of far-reaching importance. It is time that every country, where the locust or grasshopper problem is serious, should count the cost of their invasions for the last half-century, and, in order to avoid them in future, start really serious investigations of the

problem from all points of view ; the cost of such work would amount only to a small fraction of the cost of a single outbreak.

Investigations in separate countries, while they may lead to very important conclusions of general interest, cannot be considered sufficient for the solution of the locust and grasshopper problem in general. Indeed, we have seen in more than one chapter of this book that many problems of general importance can become clear only after comparing the data obtained in various countries and referring to different species. This means that a great practical step towards a general solution of the locust and grasshopper problem would lie in the organisation of research on an international scale. It would be beyond the scope of this book to formulate a definite proposal to that effect, but, broadly speaking, a central international research organisation with branches in various countries, all working on the same general lines and continually exchanging newly acquired information, would go very far in the right direction (see Vayssière, 1924).

Apart from the necessity of organising research, both local and international, by entomologists, it must be not forgotten that many problems of bionomics, ecology, etc., cannot possibly be solved by the latter, owing to the necessity of applying methods that are beyond the usual technical training of an entomologist. We know that the locust and grasshopper problem is not as narrow as might seem at the first glance ; on the contrary, it involves studies in the anatomy and functions of sense organs, in physiology generally, in heredity, etc. All these studies require very special qualifications and equipment which are seldom accessible to an entomologist, and assistance from other specialists (physiologists, geneticists, botanists) is unavoidable. To a certain extent this might be overcome by inviting the co-operation of various specialists, but there is still another way of increasing the sum total of our knowledge on ACRIDIDÆ. I have in view the possibility of utilising them as objects for research in various laboratories without any practical aims. We have seen above that certain aspects of the locust and grasshopper problem are of the widest theoretical interest to a general biologist—the phenomenon of phases is surely worth the attention of any theoretical biologist. Similarly, the ACRIDIDÆ may serve as excellent objects for studies on tropisms and reflexes, on metabolism, and on a number of other questions of general biological interest. At the present time, scientific laboratories ignore these insects (and insects generally) as " uninteresting," and work on subjects that are not more valuable from a scientific point of view and quite indifferent for practical purposes. As a result, there are excellent monographs on the anatomy, embryonic development, etc., of some of the rarest (not always the most interesting scientifically) invertebrate animals, while there is actually *not a single species* of ACRIDIDÆ the anatomy of which is known in detail. This is often explained on the ground that the anatomy of insects is not worth studying because their anatomical structures are supposed to be very uniform, but it is still difficult to see why studies on the nephridia of some rare marine worm are more scientific than research on the organs of secretion in ACRIDIDÆ, which cannot be said to be " uninteresting " since they are practically unknown.

This peculiar attitude of university and other research laboratories towards insects is, fortunately, undergoing at present some evolution, and during recent years locusts have penetrated into university laboratories as subjects of equal scientific value with Molluscs and Echinoderms. We entomologists need not insist on some special lines of investigation of our insects in research laboratories ; let specialists approach the subject with their own problems and their own methods ; let them study the anatomy, histology, chromosomes, variability, chemistry of pigments, metabolism—anything they want ; we shall be able to extract from all such material what is necessary for our special purposes, while all the rest will be as valuable for science generally, as if it was gained from other subjects. Such a co-operation of practical entomologists and of independent, purely scientific investigators would be ideal and would undoubtedly do much towards a solution of the locust and grasshopper problem, while not compromising " pure " science. In practice, this may be reached by drawing the attention of research students in anatomy, physiology, heredity, etc., to the ACRIDIDÆ as subjects easily obtainable in any numbers, not difficult to keep, and, contrary to the general opinion, very little studied in any respect.

Side by side with research in the locust and grasshopper problem on the broad lines indicated above, and more definitely set forth in corresponding chapters of this book, should go the practical work of preventing and suppressing outbreaks, which will recur from time to time until entomologists know enough to develop practical schemes for making them impossible. The technical side of this practical work, as we know, is easy, and the root of the problem is in its organisation. Without repeating what has been said in the corresponding chapters, I would only stress once more that the existing organisations are not wholly efficient anywhere. Improvements in organisations for control are practically possible almost everywhere, and with them the local grasshopper and locust problem must lose its acuteness, though its solution can come only through persistent research on a really broad scale and a world-wide basis.

BIBLIOGRAPHY

The list of papers given below does not present a full bibliography of the locust and grasshopper problem in all its branches, but consists merely of the papers that I have quoted with the addition of some works that are in the nature of compilations that I have not used since I have preferred in all cases to get my information from the original sources. Even with these limitations, the list includes well over 400 titles, in ten different languages; it is worth mentioning specially that Russian papers constitute about one-fourth of this number; this has arisen, not because of my partiality for Russian literature, but simply as a result of the relatively large number of important papers on the locust and grasshopper problem that have been published in Russia.

It would be very difficult to compile a complete bibliography of the problem, the literature on it being scattered not only in various special (entomological, zoological, and agricultural) publications, but also in numberless contributions to the general press of all countries. Judging from the fact that Künckel, as far back as 1888, counted about 500 titles, and that about the same number of titles was published by the *Institut International d'Agriculture* in 1916, while Jacobson's book, published in 1905, includes a special bibliography of the Russian literature comprising over 300 titles, it would not be unreasonable to estimate the number of titles of books and papers dealing with this problem (apart from purely systematic works) at nearly 2000.

This implies that the list compiled here includes not more than one-fifth of the whole literature, but it must be not forgotten that by far the largest portion of the latter consists of compiled articles, pamphlets, instructions for control, reports of campaigns, etc., and that these have no real value as a source of original information. I am convinced, therefore, that nothing really important has escaped my notice, though minor oversights are, of course, unavoidable.

Abeloos, M. et Toumanoff, K. 1926. Sur la présence de "carotinalbumines" chez *Carausius* (*Dixippus*) *morosus*, Br.—*Bull. Soc. zool. Fr.* **51**: 281–285.

Aldrich, J. M. 1916. *Sarcophaga* and allies in North America.—*Ent. Soc. Amer.*, Thomas Say Found. Publ. no. **1**: 301 pp. 16 pls.

1927. A new species of *Oedematocera* reared from the tropical migratory locust.—*Proc. Ent. Soc. Wash.* **29**: 17–18.

1927a. The Dipterous parasites of the migratory locust of tropical America, *Schistocerca paranensis*, Burm.—*J. Econ. Ent.* **20**: 588–593.

Alpatov, V. V. 1917. Variation statistics as applied to the systematics of the Asiatic locust. (In Russian.)—*La Défense des Plantes*, Leningrad, **3**: 352–359, 3 figs.

American Cyanamid Company. Research in the development of Cyanogas Calcium Cyanide. Sect. 7: Locusts. pp. 31–51, 6 figs. 3 charts.

Antonov, N. V. 1922. The influence of some meteorological factors on Acrididæ. (In Russian.)—*Izv. Sibirsk. Ent. Byuro*, **1**: 22–26.

Arkhangelskiĭ. 1923. Control of the Italian locust in the Merv district by means of poisoned baits. (In Russian.)—*Khlopkovoe Delo*, 1923, no. **7–8**: 130–134.

Artom, C. 1909. Cromosomi ed eterochromosomi nelle cinesi spermatogeniche di *Stauronotus maroccanus*, Thunb.—*Biologica*, Turin, **16**: 1–24, 1 pl.

Ashmead, W. H. 1893. Monograph of the North American Proctotrupidæ.—*Bull. U. S. Nat. Mus.* **45**: 472 pp. 18 pls.

Asmuss, E. P. 1858. Verzeichniss einiger Insekten in denen ich Gordiaceen angetraf.—*Wien. ent. Monatschr.* **2**: 171–181.

Baer, W. 1920–1921. Die Tachinen als Schmarotzer der schädlichen Insekten.—*Z. angew. Ent.* **6**: 185–246; **7**: 97–163, 349–423, 63 figs.

Baird, W. 1853. Catalogue of the species of Entozoa, or intestinal worms, contained in the collection of the British Museum. London. 132 pp. 2 pls.

Ball, E. D. 1915. How to control the grasshoppers.—*Bull. Utah Agric. Expt. Sta.* **138**: 79–116, 6 pls.

Ballard, E. & Muliyil, J. A. 1921. Experiments in grasshopper control by poisoned bait in South India.—*Yearb. Madras Agric. Dept.* **1920–21**: 33–45.

Baranov, N. 1924. Parasitic fly of the Moroccan locust. (In Serbian.)—*Glasnik Min. Polyoprivred. i Voda*, Beograd, 2, no. **7**: 40–54.

1925. Material for a new classification of Acridodea. (In Serbian.)—*Polyoprivred. Ogledna Kontrol. Sta. Topchider, Phyto-Ent. Odsek*, Beograd, br. **3**: 28 pp. 14 figs.

1925a. *Blaesoxypha lineata*, Fall., as a parasite of *Dociostaurus maroccanus*, Thunb. (In Russian.)—*La Défense des Plantes*, Leningrad, **2**: 130–138, 6 figs.

1925b. Notes on the morphology of Acrididæ. (In Russian.)—*T.c.*: 8–9.

Baranov, V. J. & Bei-Bienko, G. Ya. 1926. Ueber eine phyto-ökologische Charakteristik der Standorte der saltatoren Orthopteren in Altai. (In Russian, Germ. smy.)—*Izv. Zapad.-Sibirsk. Otd. Russk. Geogr. Obshch.* **5**: 179–198.

Barber, M. A. & Jones, C. R. 1915. A test of *Coccobacillus acridiorum*, d'Herelle, on locusts in the Philippines.—*Philipp. J. Sci.* Ser. B, **10**: 163–176.

Beauregard, H. 1890. Les insectes vésicants. Paris. 544 pp. 34 pls. 44 figs.

Beddard, F. E. 1907. On a new Enchytræid worm (*Henlea lefroyi*, sp. n.) from India—destructive to the eggs of a locust (*Acridium* sp.).—*J. Bombay Nat. Hist. Soc.* **17**: 797–799. (See also *Proc. Zool. Soc. Lond.* **1905**: 562–564.)

Bei-Bienko. 1926. *See* Baranov & Bei-Bienko.

1928. Synopsis of the larvæ of the West Siberian locusts. (In Russian.)—*Trud. Sibirsk. Inst. Selsk. Khoz. i Lesov.* **9**: reprint, 39 pp.

Berezhkov, R. P. 1922. The technique of the bait method of grasshopper control in Siberia and abroad. (In Russian.)—*Izv. Sibirsk. Ent. Byuro*, **1**: 16–22.

1923. Control of grasshoppers by poisoned baits. (In Russian.)—*Op. c.* **2**: 5–24.

1924. A brief review of the work of the Tomsk station for plant protection. (In Russian.)—*Op. c.* **3**: 53–60.

Berezhkova, A. A. 1924. The egg parasite of the dark-winged grasshopper (*Stenobothrus morio*, F.). (In Russian.)—*Izv. Sibirsk. Sta. Zashch. Rast. ot vredit.*, Novonikolaevsk, **1** (4): 45–47.

Berg, C. 1898. Sobre los enemigos pequeños de la langosta peregrina *Schistocerca paranensis* (Burm.).—*Comun. Mus. nac.*, Buenos Aires, **1**, no. 2: 25–30.

Berlese, A. 1893. Acari, Myriopoda et Scorpiones hujusque in Italia reperta. Ordo Prostigmata.

1900. Gli Acari agrari.—*Riv. Patol. veg.* **8**: 227–297.

1911. Acarorum species novæ quindecim.—*Redia*, **7**: 429–435.

1912. Trombidiidæ. Prospetto dei generi e delle specie finora noti.—*Redia*, **8**: 1–291.

1916. Entomophagous insects and their practical employment in agriculture.—*Int. Rev. Sci. Pract. Agric.* **7**: 321–332.

1918. Centuria quarta di Acari nuovi.—*Redia*, **13**: 116–192.

1918a. Su una nuova specie di Trombididæ appartenente ad un nuovo genere supposta parassita, allo stato di larva de Cavallette, in Puglia.—*Redia*, **13**: 93–97.

Bezrukov, J. G. 1922. A brief report on the work of the Omsk laboratory of the Siberian Entomological Bureau in 1919–1922. (In Russian.)—*Izv. Sibirsk. Ent. Byuro*, **1**: 26–30.

1923. Egg-pods of Acrididæ. (In Russian.)—*Op. c.* **2**: 25–37, 20 figs.

Blatchley, W. S. 1920. Orthoptera of North-eastern America. Indianapolis. 784 pp. 246 figs.

Bodenheimer, F. S. 1923. Die parasitären Beziehungen zwischen Würmer und Insekten.—*Centrabl. Bakt.* (2), **58**: 220–242.

Bodine, J. N. 1921. Factors influencing the water content and the rate of metabolism of certain Orthoptera.—*J. Exp. Zool.* **32**: 137–164.

1923. Hibernation in Orthoptera. I. Physiological changes during hibernation in certain Orthoptera.—*Op. c.* **37**: 457–476.

1925. Effect of temperature on rate of embryonic development of certain Orthoptera.—*Op. c.* **42**: 91–109.

1925a. Hydrogen Ion concentration in the blood of certain insects (Orthoptera).—*Biol. Bull. Woods Hole, Mass.* **51**: 363–369.

Bodkin, G. E. & Cleare, L. D. 1919. An invasion of British Guiana by locusts in 1917, with a complete illustrated account of the life history of the species.—*Bull. Ent. Res.* **9**: 341–357, 8 figs.

Boldyrev, B. Th. 1927. Some data on spermatophore fertilisation in insects. (In Russian.)—*Rev. russe Ent.* **21**: 133–136.

Bordage, E. 1914. Notes biologiques recueillies à l'île de la Réunion. iii. Sur les Acridiens de la Réunion.—*Bull. sci. Fr. Belg.* **47**: 395–396.

Bordas, L. 1897. L'appareil digestive des Orthoptères.—*Ann. Sci. nat.* (8) **5**: 1–208, 12 pls.

1898. Etude sur l'anatomie et l'histologie de rectum et des glandes rectales des Orthoptères.—*C.R. Acad. Sci. Paris*, **126**: 911–912.

1900. Contribution à l'étude du systeme nerveux sympathique sus-intestinal ou stomatogastrique des Orthoptères.—*Bull. sci. Fr. Belg.* **33**: 458–482, 2 pls.

Brèthes, J. 1912. Sobre la *Brachycoma acridiorum*, Weyenb.—*An. Mus. nac. Hist. nat. Buenos Aires*, **22**: 441–446, 3 figs.

1917. El bicho moro (*Epicauta adspersa, Ep. atomaria*).—*An. Soc. rural Argent.* **51**: 591–600.

Brues, C. T. 1917. Adult Hymenopterous parasites attached to the body of their host.—*Proc. Nat. Acad. Sci. Wash.* **3**: 136–140, 1 fig.

1917a. Note on the adult habits of some Hymenopterous egg-parasites of Orthoptera and Mantoidea.—*Psyche*, **24**: 195–196, 1 fig.

Bruner, L. 1898. The first report of the Merchants' Locust Investigation Commission of Buenos Aires. Buenos Aires, 100 pp. 27 figs, 1 pl.

1900. The second report of the Merchants' Locust Investigation Commission of Buenos Aires. Lincoln, Neb. 80 pp. 46 figs.

Bryant, H. C. 1912. Birds in relation to a grasshopper outbreak in California.—*Univ. Calif. Pub. Zool.* **11**: 1–20.

Bücher, H. 1918. (Unter Mitwirkung von V. Bauer, G. Bredemann, E. Fickendey, W. La Baume und J. Loag.) Die Heuschreckenplage und ihre Bekämpfung.—*Monog. angew. Ent.*, Berlin, **3**: 274 pp. 33 figs. 20 pls. 11 maps.

du Buisson. 1925. Observations sur la ventilation trachéenne des insectes. Première note. La ventilation trachéenne chez un Acridien.—*Bull. Acad. Belg.* Cl. Sci. (5) **10**: 373–391, 6 figs.

Bush, S. F. 1928. A study on the gregarines of the grasshoppers of Pietermaritzburg, Natal.—*Ann. Natal Mus.* **6**: 97–169, 3 pls. 3 figs.

Butler, E. J. & Lefroy, H. M. 1907. Report on trials of the South African locust fungus in India.—*Bull. Agric. Res. Inst. Pusa*, no. **5**: 5 pp.

Buxton, P. A. 1924. Heat, moisture and animal life in deserts.—*Proc. R. Soc.*, London, B, **96**: 123–131.

Buys, K. S. 1924. Adipose tissue in insects.—*J. Morph.* **38**: 485–528, 8 pls.

Camerano, L. 1897. Monographia dei Gordii.—*Mem. Acad. Sci. Torino*, **47**: 337–419, 3 pls.

Carothers, E. E. 1923. Notes on the taxonomy, development and life history of certain Acrididæ.—*Trans. Amer. Ent. Soc.* **49**: 7–24, 4 pls.

Chang, L. 1925 (?). Studies on *Pachytylus migratorioides*. (In Chinese.)

Chapman, R. N. 1927. Animal ecology with especial reference to insects. 2nd edn. Minneapolis, ix+187+183 pp. (mimeographed).

Chittenden, F. H. 1905. The cabbage hair-worm.—*Circ. U. S. Dept. Agric. Ent. Bur.* **62**: 6 pp. 1 fig.

Chopard, L. 1920. Recherches sur la conformation et le développement des derniers segments abdominaux chez les Orthoptères. (Thèse Fac. Sci. Paris.) Rennes, 352 pp. 623 figs. 7 pls.

Cobb, N. A. 1920. The species of *Mermis*.—*J. Parasit.* **13**: 66–72, 1 fig. 1 pl.

Cobb, N. A., Steiner, G. & Christie, J. R. 1923. *Agamermis decaudata*, Cobb, Steiner and Christie; a Nema parasite of grasshoppers and other insects.—*J. Agric. Res.* **23**: 921–926.

1925. The Nemic parasites of grasshoppers.—*Official Rec. U. S. Dept. Agric.* **4**, no. 25: 5.

Cobelli, R. 1886. Gli Ortotteri genuini del Trentino.—*Pubb. civ. Mus. Lovereto*, **10**: 100 pp. 1 pl.

COLEMAN, L. C. 1911. The Jola or Deccan grasshopper (*Colemania sphenarioides*, Bol.).—*Bull. Dept. Agric. Mysore, Ent. Ser.* no. **2**: 43 pp. 10 pls.

COLEMAN, L. C. & KUNHI KANNAN, K. 1911. The rice grasshopper (*Hieroglyphus banian*, F.).—*Op. c.* no. **1**: 52 pp. 5 pls.

CONIL, P. A. 1881. Études sur l'*Acridium paranense*, Burm., ses variétés et plusiers insectes qui le détruisent.—*Bol. Acad. nac. Cordoba*, **3**: 386–472, 4 pls.

COOLEY, R. A., PARKER, J. R. & SEAMANS, H. L. 1918. Grasshopper control in Montana.—*Circ. Montana Agric. Expt. Sta.* **76**: 119–147, 16 figs.

COQUILLETT, D. W. 1893. The Dipterous parasite of *Melanoplus devastator* of California.—*Insect Life*, Washington, **5**: 23.

CORKINS, C. L. 1922. Notes on the migration of *Melanoplus atlanis*, Riley, in northern North Dakota in 1920.—*Canad. Ent.* **54**: 1–4.

1923. Sodium arsenite as a killing agent in grasshopper baits.—*Bull. Colorado Agric. Expt. Sta.* **280**: 15 pp.

1923a. Grasshopper control in Colorado.—*Bull. Colorado Agric. Expt. Sta.* **287**: 19 pp. figs.

COTES, E. C. 1891. The locust of North-Western India, *Acridium peregrinum*.—*J. Bombay Nat. Hist. Soc.* **6**: 242–262, 1 pl.

CRAMPTON, G. C. 1918. Thoracic sclerites of the grasshopper *Dissosteira carolina*.—*Ann. Ent. Soc. Amer.* **11**: 347–367, 1 pl.

CRAWFORD, J. C. 1910. Two new species of African parasitic Hymenoptera.—*Canad. Ent.* **42**: 222.

1911. Descriptions of new Hymenoptera.—*Proc. U. S. Nat. Mus.* **41**, no. 1855: 268 pp.

CRAWLEY, H. 1907. The polycystid gregarines of the United States (Third contribution).—*Proc. Acad. Nat. Sci. Philadelphia*, **59**: 220–228, 1 pl.

CUÉNOT, L. 1896. Etudes physiologiques sur les Orthoptères.—*Arch. Biol.* **14**: 293–341.

DAMPF, A. 1925. *See* HOFFMANN, DAMPF & VARELA.

1926. Der Färbungswechsel bei den Wanderheuschreckenlarven, ein biologisches Rätsel.—*Verh. III. Int. Ent. Kongr. Zürich*, **2**: 276–290, 1 pl.

DAVIS, H. 1908. Spermatogenesis in Acrididæ and Locustidæ.—*Bull. Mus. Comp. Zool. Harvard*, **43**: no. 2.

DEMOLL, R. & SCHEURING, L. 1912. Die Bedeutung der Ocellen der Insekten.—*Zool. Jahrb.*, Abt. allg. Zool. u. Physiol. **31**: 519–628, 23 figs.

DEPDOLLA, PH. 1917. Die Keimzellenbildung und die Befruchtung bei den Insekten.—SCHRÖDER, *Handb. Ent.* **1**: 825–1116.

DE STEFANI PEREZ, T. 1889. Una nota sulla *Chalcis dalmanni*.—*Naturalisto sicil.*, Palermo, **9**: 11–12.

1891. De duobus novis hymenopteris Siciliæ.—*Op. c.* **10**: 117–119.

1912. Le cavalette ed alcuno loro parasiti.—*Boll. Min. Agric. Ind. e Comm.*, Rome (C), **2**: fasc. **2–3**: pp. 30–52, 17 figs. 4 pls.

1913. Cavalette, loro invasioni e lotta contro di esse in Sicilia.—*Giorn. Sci. nat. econ. Palermo*, **30**: 117–199, 21 figs.

DIESING, K. M. 1851. Systema helminthum. **2**. Vindobona; vi+588 pp.

1859. Revision des Rhyngodeen.—*Sitz. Ber. Akad. Wiss. Wien*, mat.-nat. Kl. **37**: 719–782, 3 pls.

DOBROVOLSKIĬ, N. A. 1921. Insect pests in the Kuban province after observations in 1921. (In Russian.)—*Bull. 3-go Ent.-Phyt. S'ezda Petrograd*, **7**: 4–7.

DODD, A. P. 1913. Australian Hymenoptera. Proctotrypoidea. No. 1. Family Scelionidæ.—*Proc. R. Soc. S. Australia*, **37**: 130–181.

1914. Further new genera and species of Australian Proctotrypoidea.—*Proc. R. Soc. Queensland*, **26**: 91–140.

DOVNAR-ZAPOLSKIĬ, D. P. 1925. Observations on the biology of *Calliptamus italicus*. (In Russian.)—*Bull. Rostovo-Nachitchevan. Sel.-Khoz. Opuit. Sta., Ent. Otd.* no. **166**: 20 pp.

1926. On grasshopper larvæ. (In Russian.)—*Izv. Severo-Kavkaz. Kraev. Sta. Zashch. Rast.* no. **2**: 153–172.

DUFOUR, L. 1837. Recherches sur quelques entozoaires et larves parasite des insectes. Orthoptères et Hyménoptères.—*Ann. Sci. Nat.* (2) **7**: 5–20, 1 pl.

1841. Recherches anatomiques et physiologiques sur les Orthoptères, les Hyménoptères et les Nevroptéres.—*Mem. Acad. Sci. Paris*, **7**: 265–647, 13 pls.

Du Porte, E. M. & Vanderleck, J. 1917. Studies on *Coccobacillus acridiorum*, d'Herelle, and on certain intestinal organisms of locusts.—*Ann. Ent. Soc. Amer.* **10**: 47–62.

Egypt. Ministry of Agriculture. 1916. Report on the great invasion of locusts in Egypt in 1915 and the measures adopted to deal with it. Cairo, 72 pp. 14 pls.

Eisentraut, M. 1926. Die spermatogonialen Teilungen bei Acridiern mit besonderer Berücksichtigung der Ueberkreuzungsfiguren.—*Z. wiss. Zool.* **127**: 141–183, 2 pls. 24 figs.

1927. Beitrag zur Frage der Farbenanpassung der Orthopteren an die Färbung der Umgebung. I. Die Farbenvariationen von *Oedipoda coerulescens* und ihre Beziehung zur Bodenfarbe.—*Z. Morph. Ökol. Tiere*, **7**: 609–642, 10 figs.

Ellis, M. M. 1913. Gregarines from some Michigan Orthoptera.—*Zool. Anz.* **43**: 78–84.

Engelhardt, V. M. 1925. The Far Eastern wingless grasshopper, *Prumna primnoa*, Fisch.-Waldh., as a pest of agriculture in the Far East. (In Russian.)—*La Défense des Plantes*, Leningrad, **2**: 298–300.

Ewing, H. E. 1904. The functions of the nervous system, with special regard to respiration, in Acrididæ.—*Kansas Univ. Sci. Bull.* **2**: 305–309.

1924. New Tarsonemid mites.—*Proc. Ent. Soc. Wash.* **26**: 67–68.

Fantham, H. B. 1923–1925. Some parasitic Protozoa found in South Africa.—*S. Afr. J. Sci.* **20**: 493–500; **21**: 438–439; **22**: 346–354.

Faure, J. C. 1923. The life history of the brown locust.—*Bull. Transvaal Univ. Coll.*, Pretoria, no. **4**: 30 pp. 2 pls.

Fedtchenko, B. A. 1874. Zoological observations on the anatomy of round worms. (In Russian.)—*Izv. Imp. Obshch. Liubit. Estest. Antrop. Etnogr. Moskva*, **10** (2): 51–68, 1 pl. 5 figs.

Fénard, A. 1896. Recherches sur les organes complémentaires internes de l'appareil génital des Orthoptères.—*Bull. sci. Fr. Belg.* **29**: 390–532, 4 pls.

Ferton, C. 1903. Notes détachées sur l'instinct des Hyménoptères mellifères et ravisseurs.—*Ann. Soc. ent. Fr.* **71** (1902): 500–531, 1 pl.

Filipjev, I. N. 1926. Injurious insects and other animals in the U.S.S.R. in 1921–1924. Part 2. Acrididæ. (In Russian.)—*Trud. Otd. priklad. Entom. Gosud. Inst. Opuit. Agron.* **13**: 57–176, 12 maps.

1926a. *Locusta migratoria* in Western Europe. (In Russian.)—*Rev. russe Ent.* **20**: 245–249, 1 map.

Fletcher, T. B. 1916. One hundred notes on Indian insects.—*Bull. Agric. Res. Inst. Pusa*, **59**: 17 pp.

Ford, A. L. 1921. The effect of poison bran mash on grasshoppers and the lapse of time between poisoning and death.—*J. Econ. Entom.* **14**: 281–285.

Ford, A. L. & Larrimer, W. H. 1921. Observations on the attractiveness of materials used in grasshopper baits.—*T.c.* 285–291.

1921a. Some factors influencing the efficiency of grasshopper baits.—*T.c.* 292–299.

Ford, Norma. 1922. An undescribed planidium of *Perilampus* from *Conocephalus*.—*Canad. Ent.* **54**: 199–204, 1 fig.

1923. A comparative study of the abdominal musculature of Orthopteroid insects.—*Trans. R. Canad. Inst.* **14**: 207–319, pls. vii–xxiii.

Frauenfeld, G. R. 1868. Zoologische Miscellen.—*Verh. zool.-bot. Ges. Wien*, **18**: 889.

Froggatt, W. W. 1903. Locusts and grasshoppers. Part I.—*Agric. Gaz. N. S. Wales*, **14**: 1102–1110, 1 pl.

1907. The eastern plague locust (*Oedaleus senegalensis*, Krauss.).—*Op. c.* **18**: 539–541.

1910. Locusts in Australia and other countries.—*Fmrs.' Bull. Dept. Agric. N. S. Wales*, no. **29**: 40 pp. 12 figs.

1912. Presidential address.—*Proc. Linn. Soc. N.S. Wales*, **37**: 23–24.

Fruhstorfer, H. 1921. Die Orthopteren der Schweiz.—*Arch. Naturgesch.* **87**: Abt. A, Heft 5; 262 pp.

Fulton, B. B. 1920. Grasshopper control in Oregon.—*3rd Crop Pest & Hort. Rep.* 1915–20, *Oregon Agric. Coll.*: 109–115.

Gause, G. F. 1928. Zur Kenntnis der Varibilität der Wanderheuschrecke (*Locusta migratoria*, L.).—*Z. angew. Ent.* **13**: 248–266.

GIARDINA, A. 1901. Funzionamento dell'armatura genitale femminile e considerazioni intorno alle ooteche degli Acridii.—*Giorn. Sci. nat. econ. Palermo,* **23**: 54–61, 8 figs.

GIRAULT, A. A. 1913. A new Scelionid from Queensland, Australia, parasitic on Acridiid eggs, with diagnosis of Australian species.—*Proc. Ent. Soc. Washington,* **15**: 4–8.

1913a. Notes on a plague of locusts in North Queensland and its relation to sugar cane.—*Societas Ent.*, Stuttgart, **28**: 45–46, 49–50.

1914. A new Scelionid parasite of locust eggs from the Northern Territory of Australia.—*Entomologist,* **47**: 197.

GLASER, R. W. 1918. A systematic study of the organisms distributed under the name of *Coccobacillus acridiorum,* d'Herelle.—*Ann. Ent. Soc. Amer.* **11**: 19–42.

1918a. On the existence of immunity principles in insects.—*Psyche,* **25**: 39–46.

GLASER, R. W. & WILCOX, A. M. 1918. On the occurrence of a *Mermis* epidemic among grasshoppers.—*Psyche,* **25**: 12–15, 1 pl.

GRABER, V. 1871. Ueber den Ursprung und Bau der Tonapparate bei den Acridiern.—*Verh. zool.-bot. Ges. Wien,* **21**: 1096–1102, 1 pl.

1873. Über den propulsatorishen Apparat der Insekten.—*Arch. mikr. Anat.* **9**: 129–196, 3 pls.

1873a. Über die Blutkörperchen der Insekten.—*Sitz. Ber. Akad. Wiss. Wien,* mat.-nat. Kl. **64**: 9–44.

1876. Ueber den pulsierenden Bauchsinus der Insekten.—*Arch. mikr. Anat.* **12**: 575–582, 1 pl.

1876a. Die tympanalen Sinnesorgane der Orthoptera.—*Denkschr. Akad. Wiss. Wien,* **36** (2): 1–140, 10 pls.

1882. Die chordotonalen Sinnesorgane und das Gehör der Insekten.—*Arch. mikr. Anat.* **20**: 506–540; **21**: 65–145, pls. figs.

GRASSÉ, P. 1922. Étude biologique sur le criquet égyptien (*Orthacanthacris aegyptia,* L.).—*Bull. biol. Fr. Belg.* **56**: 545–578, 7 figs.

1923. Sur la phototropisme des quelques criquets.—*C.R. Soc. Biol.* **89**: 898–899, 1 fig.

1923–24. La biologie des Acridiens ravageurs français.—*Revue Zool. agric.*, Bordeaux, **22**: 268–282, 297–314; **23**: 1–14, 57–65, 1 pl. 17 figs.

1924. Notes sur quelques Orthoptères français, ii. Le cycle annuel des Acridiens.—*Bull. Soc. ent. Fr.* **1924**: 45–47.

GREENE, C. T. 1927. The larva and puparium of *Oedematocera dampfi,* Aldrich.—*Proc. Ent. Soc. Washington,* **29**: 18–19, 1 fig.

GURNEY, W. B. 1908. Notes on grasshopper (or locust) swarms in N. S. Wales during 1907–1908.—*Agric. Gaz. N. S. Wales,* **19**: 411–419, 6 figs. 1 pl.

1925. Grasshopper swarms and their control.—*Op. c.* **36**: 635–640, 6 figs.

HAGMEIER, A. 1912. Beiträge zur Kenntniss der Mermithiden.—*Zool. Jahrb.*, Syst. **32**: 521–612, pls. 17–21.

HALL, M. C. 1907. A study of some gregarines with especial reference to *Hirmocystis rigida,* n. sp.—*Univ. Nebraska Studies,* **7**: 149–174, 1 pl.

HANCOCK, J. L. 1894. Unusual flights of the grouse locust (*Tettigidea lateralis,* Say) in north eastern Illinois.—*Amer. Nat.* **28**: 483–487, 1 pl.

1898. The food habits of the Tettigidæ.—*Ent. Rec. & J. Var.* **10**: 6–7.

1902. The Tettigidæ of North America. Chicago. 188 pp. 11 pls.

HEBARD, M. 1923. Studies in the Dermaptera and Orthoptera of Colombia. Third paper. Orthopterous family Acrididæ.—*Trans. Amer. Ent. Soc.* **49**: 165–313, 17 pls.

1925. The Orthoptera of South Dakota.—*Proc. Acad. Nat. Sci. Philadelphia,* **77**: 33–155.

1925a. Dermaptera and Orthoptera from the state of Sinaloa, Mexico. Part II. Saltatorial Orthoptera.—*Trans. Amer. Ent. Soc.* **51**: 285–287.

D'HERELLE, F. 1911. Sur une épizootie de nature bactérienne sévissant sur les sauterelles au Mexique.—*C.R. Acad. Sci. Paris,* **152**: 1415–1416.

1914. Le coccobacille des sauterelles.—*Ann. Inst. Pasteur,* Paris, **28**: 281–328, 387–404.

HERNANDEZ, A. 1921. Locust extermination. *20th Rep. Philipp. Bur. Agric.* **1920,** 47–48.

HERRICK, G. W. & HADLEY, C. H. 1916. The lesser migratory locust.—*Bull. Cornell Univ. Agric. Expt. Sta.* **378**: 45 pp. 17 figs.

HEYMONS, R. 1895. Die Embryonalentwickelung von Dermapteren und Orthopteren unter besonderer Berücksichtigung der Keimblätterbildung. Jena. vi+136 pp. 12 pls. 33 figs.

HINGSTON, R. W. G. 1927. The liquid-squirting habit of Oriental grasshoppers.—*Trans. Ent. Soc. London*, **75**: 65–68, 1 pl.

HIRST, S. 1921. On some new parasitic mites.—*Proc. Zool. Soc. London*, **1921**: 800, fig. 4.

HOFFMANN, C. C. 1925. Las migraciones de la langosta (*Schistocerca paranensis*, Burm.) y contribucion al conocimiento de sus movimientos en Mexico.—*Mem. Soc. Ant. Alzate*, Mexico, **44**: 191–227.

HOFFMANN, C. C., DAMPF, A. & VARELA. 1925. Informe de la Comision cientifica exploradora de la plaga de la langosta en el Estado de Veracruz.—*Monog. Inst. Hyg. Mexico*, **3**: 140 pp. 46 pls.

HOLLANDE, A. CH. 1919. Formes lévures pathogènes observées dans le sang d'Acridium (*Caloptenus italicus*, L.).—*C.R. Acad. Sci. Paris*, **168**: 1341–1344.

1925. Les cellules à urates des Acridiens Orthoptères et la genèse de ces urates.—*Op. c.* **181**: 1175–1176.

1926. La signification de l'autohémorrhée des insectes.—*Arch. Anat. microsc.* **22**: 374–412, 16 figs.

HOLLANDE, A. CH. & MOREAU, F. 1922. Présence des formes-lévures bourgeonnantes dans le sang des *Stenobothrus* (Orthoptères), leur évolution par culture en un champignon entomophyte: *Isaria stenobothri*, n. sp.—*Arch. zool. exp. gén.* **61**: 59–74, figs.

HOWARD, C. W. 1910. Locust destruction in South Africa.—*J. Econ. Ent.* **3**: 260–272, 2 maps, 1 pl.

1918. A preliminary report on the Trombidiidæ of Minnesota.—*17th Rep. State Ent. Minnesota*: 111–144, 7 pls.

HUNTER, S. J. 1899. Alfalfa, grasshoppers, bees; their relationship.—*Bull. Dept. Ent. Univ. Kansas*, [**6**]: pt. 1, 64 pp. 8 pls. 30 figs.

HUTSON, J. C. 1926. The Spotted Locust, *Aularches miliaris*, L.—*Yearb. Dept. Agric. Ceylon*, **1926**: 36–44, 1 pl.

INGENITSKIĬ, I. V. 1896. Egg-pods and larvæ of some Acrididæ. (In Russian.)—Derevnia, **1896**, no. 7: 582–589 (also published separately: St. Petersburg, 1896, 8 pp.).

1898. On the Acrididæ of Eastern Siberia and their parasites. (In Russian.)—*Horae Soc. Ent. Ross.* **32**: p. liii.

INSTITUT INTERNATIONAL D'AGRICULTURE. 1916. La lutte contre les sauterelles dans les diverses pays.—Rome, xvi+187 pp.

1921. Actes de la Conférence Internationale pour l'organisation de la lutte contre les sauterelles (Rome, 28–31 Octobre 1920).—Rome, 171 pp.

1926. État actuel de l'organisation de la lutte contre les sauterelles dans divers pays.—Rome, 131 pp.

ITO, HIROWO. 1924. Contribution histologique et physiologique à l'étude des annexes des organes genitaux des Orthoptères. (Thèse Fac. Sci. Univ. Montpellier.) Paris, 118 pp. 17 figs. 6 pls.

IWANOWA, S. A. 1925. Zur Frage uber die Spermatophorenbefruchtung bei den Acridiodea (*Locusta migratoria*, L.).—*Zool. Anz.* **65**: 75–86, 10 figs.

1926. The structure of the inner genital apparatus of the male of *Locusta migratoria*, L. (Formation of a spermatophore in Acrididæ.) (In Russian.)—*Utchen. Zapiski Kazan. Gosud. Univ.* **86**: Pt. I, 2 (Nat. Sci.): 50–56, 4 figs.

JABLONOWSKI, J. 1926. Ungarns Heuschreckengefahr einst und jetzt; eine entomologish-biologische Skizze.—*Verh. III. Intern. Ent. Kongr. Zürich*: 377–388.

JACKSON, F. V. 1926. Locust campaign.—*Mon. Agric. Bull. Iraq*, 16th Nov.–15th Dec. 1 p.

JATZENTKOWSKIĬ, E. V. 1913. Some data on the biology of the locust (*Pachytylus migratorius*, L.). (In Russian.)—*Rev. russe Ent.* **13**: 323–335, 11 figs.

JOHNSTON, H. B. 1924. A note on locusts.—*Sudan Notes & Records*, **7**: No. 2: 91–101, 2 pls. 2 figs.

1926. A further contribution to our knowledge of the bionomics and control of the migratory locust, *Schistocerca gregaria* (*peregrina*, Ol.) in the Sudan.—*Bull. Ent. Sect. Wellcome Trop. Res. Lab.* no. **22**: 14 pp. 1 map.

Jones, V. 1921. The grasshopper pest. How to overcome it by co-operative campaigns.—*Bull. Extens. Div. Univ. Idaho*, no. **52**: 19 pp. 13 figs.

Jörschke, H. 1914. Die Facettenaugen der Orthopteren und Termiten.—*Z. wiss. Zool.* **111**: 153–280, 57 figs. 1 pl.

Karny, H. 1908. Über das Schnarren der Heuschrecken.—*Stett. ent. Ztg.* **49**: 112–119.

1912. Über die Reduktion der Flugorgane bei den Orthopteren.—*Zool. Jahrb. Abt. allg. Zool. u. Physiol.* **33**: 27–40, 2 pls.

1924. Beiträge zur Malayischen Orthopterenfauna. IV. Zur Entwickelung von *Acrida turrita*, L.—*Treubia*, **5**: 1–3, figs.

Keppen, F. P. 1870. On locusts and other injurious Orthoptera of the family Acridiæ, mainly with reference to Russia. (In Russian.)—*Trud. Russk. Ent. Obshch.* **5**: 381 pp. 1 map.

Kelly, E. O. G. 1914. A new Sarcophagid parasite of grasshoppers.—*J. Agric. Res.* **2**: 435–446, 1 pl.

Kharin, S. 1925. Some data on the control of the Asiatic locust by poisoned baits in summer 1923. (In Russian.)—*Brief Rep. Dzhetysu Reg. Byuro*, Almaata: 69–75.

King, H. H. 1917. The migratory locust (*Schistocerca peregrina*, Oliv.) and its control in the Anglo-Egyptian Sudan, 1915. (In English and Arabic.)—[Wellcome Trop. Res. Lab. Ent. Bull. **3**.] Khartoum, 12 pp. 1 map.

1922. Note on the origin of the migratory locust.—*Sudan Notes & Records*, **5**: 54–56.

Kiritchenko, Alexei. 1926. Materials on the ecology and biology of *Calliptamus italicus*, L. in the steppe zone of Ukraine. (In Russian.)—*Odessa Agric. Expt. Sta. Ent. Dept.* **1**: 47 pp. 2 pls.

Kleine, R. 1909. Zur Kenntniss der Diptera.—*Z. Naturwiss.* **81**: 194.

Korotkich, G. I. 1927. First aviation expedition for the control of locusts. (In Russian.)—*La Défense des Plantes*, Leningrad, **3**: 479–518, 18 figs.

Kowalewsky, A. 1894. Études sur le cœur de quelques Orthoptères.—*Arch. zool. exp.* (3) **2**: 485.

1894a. Études experimentales sur les glandes lymphatiques des Invertébrés.—*Bull. Acad. imp. Sci. St. Petersb.* N.S. **4**: 273–295.

Kozminski, Z. 1925. Ökologische Untersuchungen an Orthopteren des Urwaldes von Bialowieza.—*Bull. Acad. polon. Sci. Lett.*, Cracovie; (B) Sci. Nat. **1925**: 447–475.

Krasilshchik, I. M. 1886. Locusts in the delta of Donau. A preliminary report on the excursion in spring 1886 for investigation on locusts in the Izmail district and in Rumania. (In Russian.)—*Trud. Odessk. Ent. Kommiss.* **1886**: 21 pp.

1893. The law of periodicity of locusts. (In Russian.)—*Odesskii Listok*, **230**: reprint, 4 pp.

Kraus, R. 1916. Zur Frage der Bekämpfung der Heuschrecken mittels des *Coccobacillus acridiorum*, d'Herelle.—*Centralbl. Bakt.* (2) **45**: 594–599.

Krogh, A. 1913. The composition of the air in the tracheal system of insects.—*Skand. Arch. Physiol.* **29**: 29–36.

Kufferath, M. H. 1921. Microbe pathogéne pour les sauterelles et d'autres insectes, *Micrococcus* (*Staphylococcus*) *acridicida*, Kufferath, nov. spec.—*Ann. Gembloux*, **27**: 253–257.

Kulagin, N. M. 1921. On the appearances of locusts in XVIII and XIX centuries in Europe. (In Russian.)—*Trud. Vtorog. Vseross. ent.-Phyt. S'ezda*: 109–122.

1923. On the development of certain species of Acrididæ. (In Russian.)—*Bull. Soc. entom. Moscou*, **2**, no. 2: 1–11, 4 pls.

Künckel d'Herculais, J. P. A. Invasions des Acridiens vulgo Sauterelles en Algérie. Alger, 2 vols. 1893–1905, 34 pls., maps, tabl.

1899. La mue chez les insectes considerée comme moyen de défense contre les parasites vegetaux ou animaux.—*C.R. Acad. Sci. Paris*, **128**: 620–622.

1907. Un Diptère vivipare de la famille des Muscides à larves tantôt parasites, tantôt végétariennes.—*Op. c.* **144**: 390–393.

La Baume, W. 1910. Die afrikanischen Wanderheuschrecken.—*Beih. Tropenpflanzer*, **11**: 65–128, 4 pls. 10 figs.

1918. *See* Bücher and others, 1918.

LAHILLE, F. 1907. La langosta y sus moscas parasitarias.—*An. Min. Agric. Argentina, Sec. Zootech.* Buenos Aires, **3** : no. 4, 136 pp. 29 figs. 7 pls.

1920. La langosta en la Republica Argentina.—*Min. Agric. Buenos Aires,* 172 pp. 16 figs. pls. maps.

LANGFORD, G. S. 1926. The possibilities of sodium fluosilicate as a poison in grasshopper baits.—*J. Econ. Ent.* **19** : 670.

LANKESTER, E. R. 1863. On our present knowledge of the Gregarinidæ.—*Quart. J. Micr. Sci.* **3** : 83–96.

LAPAZARAN Y BERISTAIN. J. C. 1925. La plaga de la langosta en la region Aragónesa.—Zaragoza. 134 pp. figs.

LEBEDEV, F. N. 1922. Experiments in the use of asphyxiating substances in the extermination of locusts. (In Russian.)—*Trud. 3-go Vseross. ent.-Phyt. S'ezda :* 1–8.

1923. How the Asiatic locust lives and feeds. (In Russian.)—Samara. 33 pp. 2 pls.

LEBEDEVA, E. A. 1925. The diagnostics of stages of Acridid larvæ. (In Russian.)—*La Défense des Plantes,* Leningrad, **2** : 309–311.

LEE, M. O. 1925. On the mechanism of respiration in certain Orthoptera.—*J. Exp. Zool.,* Philadelphia, **41** : 125–154.

LEFROY, H. M. 1907. Locusts in India.—*Agric. J. India,* **2** : 237–245, 7 pls.

1906. The Bombay locust (*Acridium succinctum,* L.).—*Mem. Dep. Agric. India, Ent. Ser.* **4** : 1–109, 13 pls.

LEGER, L. 1893. Sur une gregarine nouvelle des Acridiens d'Algérie.—*C.R. Acad. Sci. Paris,* **117** : 811–813.

LEIDY, J. 1851. On the Gordiaceæ.—*Proc. Acad. Nat. Sci. Philadelphia,* **5** : 262–263, 266, 275.

1853. On the organisation of the genus *Gregarina* of Dufour.—*Trans. Amer. Phil. Soc.* N.S. **10** : 233–240, 2 pls. 41 figs.

1856. A synopsis of Entozoa and some of their ecto-congeners observed by the author.—*Proc. Acad. Nat. Sci. Philadelphia,* **8** : 42–58.

LEONARDI, G. 1899. Una nuove specie di *Trombidium* (*T. debilipes,* Leon.) parassita, allo stato larvale, del *Pachytylus migratorius,* L.—*Riv. Patol. veg.* **8** : 367–369, 1 pl.

DE LEPINEY, J. 1928. Sur le comportement de *Schistocerca gregaria,* Forsk. au cours des vols.—*Rev. path. vég. ent. agric.* Mars **1928** : reprint, 15 pp.

LINK, E. 1909. Über die Stirnaugen der hemimetabolen Insekten.—*Zool. Jahrb. Abt. Anat.* **27** : 281–376, 14 figs. 4 pls.

VON LINSTOW, O. F. B. 1892. Uber *Mermis nigrescens,* Duj.—*Arch. mikr. Anat. Bonn,* **40** : 498–512, 2 pls. 14 figs.

1897. Helminthologische Mitteilungen.—*Op. c.* **48** : 375–397, 2 pls. 34 figs.

1898. Das Genus *Mermis.*—*Op. c.* **53** (2) : 149–168, 1 pl. 22 figs.

LIZER, C. 1919. Informe sobre la expedicion al Chaco Boliviano presentado al 1a Comisión de Defensa Agricola.—*Bol. Min. Agric. Buenos Aires,* **29** : 26–70, 4 maps.

LOCKWOOD, S. 1924. Estimating the abundance of, and damage done by grasshoppers. —*J. Econ. Ent.* **17** : 197–202.

LOUNSBURY, C. P. 1910. *See* S. African Central Locust Bureau, Fourth Report.

1915. Some phases of the locust problem.—*S. Afr. J. Sci.* **12** : 33–45.

1924. Report of the Department of Agriculture. X. Entomology.—*J. Dept. Agr. Un. S. Afr.* **9** : 556–567.

LÖW, H. 1861. *Blaesoxipha grylloctona,* nov. genus et species.—*Wien. ent. Monatschr.* **5** : 384–387.

LUKIANOVITCH, F. K. 1925.—On the appearance of the Asiatic locust in the late Poltava province.—*Zakhist Roslin,* Kharkov, **1**, no. 5–6 : 51–53.

LYNCH ARRIBALZAGA, E. 1903. La langosta voladora del Perú.—*Ann. Mus. nac. Hist. nat. Buenos Aires,* (3) **2** : 1–5.

1918. La langosta voladora de Colombia y Venezuela. *Physis,* Buenos Aires, **4** : 49–79, 2 figs.

MAKALOWSKAJA, W. N. 1925. Zur Biologie der *Locusta migratoria* (Wanderheuschrecke). —*Zool. Anz.* **44** : 295–306, 3 figs.

MALAN, D. J. & MALAN, D. E. 1925. The spermatogenesis of *Locustana pardalina* (Walker) (The brown trek locust).—*Trans. R. Soc. S. Africa,* **13** : reprint, 22 pp. 2 pls.

Malenotti, E. 1922. La difesa antiacridica in provincia di Aquila nel 1921.—*R. Osserv. Fitopat.* Verona, 24 pp.

Mally, C. W. 1923. Arsenite of soda as a locust poison.—*J. Dept. Agric. Un. S. Afr.* **6**: 220–232, 6 figs.

Maltzev, M. V. 1914. Experiments in breeding the migratory locust (*Pachytylus migratorius*, L.) under artificial conditions. (In Russian.)—*Trud. Sel.-khoz. bact. Lab. Glavn. Upravl. Zeml.* **5**, no. 15: 25 pp. 19 figs.

1925. On the number of egg-pods in the females of some species of Acrididæ. (In Russian.)—*La Défense des Plantes*, Leningrad, **2**: 301–306.

Mann, H. H. & Burns, W. 1927. The locust attack of 1926–27 in Sind, Kathiavar and Gujarat.—*Agric. J. India*, **22**: 325–332.

Marelli, C. 1916. Las diferentes larvas de langostas que acompañan a las grandes mangas de la saltona de *Schistocerca paranensis*, Burm.—*An. Mus. nac. Hist. nat. Buenos Aires*, **28**: 345–390.

Martinez y Fernandez-Castillo, A. 1912. Anatomia e histologia del *Ocnerodes brunnerii*, Bol.—*Trab. Mus. Cien. nat. Madrid*, no. **4**: 40 pp. 24 figs.; no. **8**: 50 pp. 47 figs.

Massini, P. C. 1917. Destruccion de la langosta. Lucha biologica.—*An. Soc. rural Argent.* **51**: 309–314.

Matsumura. 1910. Die schädlichen und nützlichen Insekten von Zuckerrohr Formosas. Tokyo. 52+86 pp. 30 pls.

May, H. G. 1920. Contributions to the life histories of *Gordius robustus*, Leidy, and *Paragordius varius* (Leidy).—*Illinois Biol. Monogr.* **5**, no. 2: 118 pp. 21 pls.

McClung, C. E. 1914. A comparative study of the chromosomes in Orthopteran spermatogenesis.—*J. Morph.* **25**: 651–729, 10 pls.

1917. The multiple chromosomes of *Hesperotettix* and *Mermiria*.—*Op. c.* **29**: 519–590, 8 pls.

1927. Synapsis and related phenomena in *Mecostethus* and *Leptysma*.—*Op. c.* **43**: 181–251, 4 pls.

McIndoo, N. E. 1920. The olfactory sense of Orthoptera.—*J. Comp. Neurol.* **31**: 405–427, 92 figs.

Merezhkovskiĭ, S. S. 1925. On the bacillus (*Coccobacillus acridiorum*) offered by d'Herelle for the extermination of the locust. (In Russian.)—*Izv. Inst. Opuit. Agron.* **3**, no. 1: 7–13.

Michael, A. D. 1899. Acari of the lake Urmi.—*J. Linn. Soc. London* (Zool.), **27**: 407.

Mikhelson, I. Ya. 1922. Observations on the migratory locust. (In Russian.)—*Bull. Soc. Ent. Moscou*, **2**, no. 1: 7–67.

Mitchener, A. V. 1921. Poisoning grasshoppers.—*Circ. Manitoba Agric. Coll.* no. **59**.

Modestov, V. 1921. Report on the control of Acrididæ in the Uralsk province in 1915. (In Russian.)—*Izv. Petrovsk. Selskokhoz. Akad.*, Moscow, **1919**, pt. 1–4: 62–84.

Montgomery, T. H. 1898. The Gordiacea of certain American collections with particular reference to the North American fauna.—*Bull. Mus. Comp. Zool. Harvard*, **32** (3): 23–59, 15 pls. 123 figs.

Montgomery, T. H., junr. 1907. The distribution of North American Gordiacea, with description of new species.—*Proc. Acad. Nat. Sci. Philadelphia*, **59**: 270–272.

Morgan, H. A. 1901. The differential grasshopper in the Mississippi Delta. Other common species.—*Bull. Div. Ent. U.S. Dept. Agric.* N.S. **30**: 7–33, 19 figs.

Moritz, L. D. 1914. Biological observations on the Italian locust, *Caloptenus* (*Calliptamus*) *italicus*, L. (In Russian.)—*Lyubitel Prirodui*, St. Petersburg, **1914**: reprint, 12 pp.

1915. Biological observations on Acrididæ of the Turgai province. (In Russian.)—*Op. c.* **1915**: reprint, 29 pp. 9 figs. 2 pls.

Moritz-Romanova, Z. E. 1925. Baits in the control of the Asiatic locust.—Tashkent, 28 pp. 2 diagr.

Morrill, A. W. 1919. The value of molasses and syrups in poisoned baits for grasshoppers and cutworms.—*J. Econ. Entom.* **12**: 337–343.

Morse, A. P. 1904. Researches on North American Acridiidæ.—*Carnegie Inst. Wash. Pub.* no. **18**: 56 pp. 8 pls.

1907. Further researches on North American Acridiidæ.—*Op. c.* **68**: 54 pp. 9 pls.

MORSTATT, H. 1921. Die Ursache der Heuschreckenplage in Ostafrica.—*Kosmos*, **1921** : Heft 3.

MUIR, F. & SWEZEY, O. H. 1927. Entomology.—*Rep. Comm. Expt. Sta. Hawaiian Sugar Plant. Ass.* **1925–26** : 16–19.

NABOURS, R. K. 1919. Parthenogenesis and crossing over in the grouse locust, *Apotettix*. —*Amer. Nat.* **53** : 131–142.

1925. Studies of inheritance and evolution in Orthoptera. V. The grouse locust, *Apotettix eurycephalus*, Hancock.—*Tech. Bull. Kansas Agric. Expt. Sta.* **17** : 231 pp. 1 pl.

NAGEL, W. 1894. Vergreichend-physiologische und anatomische Untersuchungen über den Geruchs- und Geschmacksinn und ihre Organe mit einleitenden Betrachtungen aus der allegemeinen vergleichenden Sinnesphysiologie.—*Bibliotheka Zoologica*, **18**.

NEWMAN, L. J. 1924. The plague locust. *J. Dept. Agric. W. Australia*, (2) **1** : 190–208, 7 figs.

NIKOLSKIĬ, V. V. 1911. The Migratory or Asiatic locust in the Syr-Darya province. (In Russian.)—*Zashch. Rast. ot vred.* (Suppmt. *Lyubit. Prirodui*), St. Petersburg, no. **3** (7) : 1–13, figs.

1913. Causes of movements of hoppers and problems in the biology of the Asiatic locust.—*Izv. Turkestan. Opuit. Sta.* Tashkent, reprint, 30 pp.

1918. Causes of movements of hoppers of the Asiatic locust. (In Russian.)—*Turkestan. Selsk. Khoz.* **1918**, no. 3–4 : reprint, 12 pp.

1923. New problems in the study of Acrididæ. (In Russian.)—*Khlopkovoe Delo*, Moscow, **1923**, no. 7–8 : 33–54.

1925. The Asiatic Locust. (In Russian.)—Leningrad. 330 pp. figs.

NOCEDO, C. 1918. Dipteros nuevos parásitos de la langosta (*Schistocerca peregrina*).—*Rev. Agric. Mexico*, **2** : 132–135, 183–186, 1 fig.

NOWAKOWSKIĬ, L. 1882. Entomophthoreæ.—*Botan. Ztg.* **1882** : 560.

OGLOBLIN. A. A. 1927. Two new Scelionid parasites of *Locusta migratoria* from Russia. —*Bull. Ent. Res.* **17** : 393–404, 7 figs.

OLIFFE, A. S. 1891. The fly-parasite of the plague locust.—*Agric. Gaz. N. S. Wales*, **2** : 255–257, 5 figs.

OUDEMANS, A. C. 1912. Die bis jetzt bekannten Larven von Trombidiidæ und Erythræidæ.—*Zool. Jahrb. Suppmt.* **14** : 230 pp.

PACKARD. 1878. *See* U.S. Entomological Commission, First Report.

PANTEL, J. 1898. Le *Thrixidion halideyanum*, Rond. Essai monographique sur les charactères extérieurs, la biologie et l'anatomie d'une larve parasite du groupe des Tachinaires.—*La Cellule*, **15**, fasc. 1 : 1–290, pls.

PAOLI, G. 1910. Sulla *Sarcophaga lineata*, Fallen, parassitta dello *Stauronotus maroccanus* (Thunb.) in Sardegna.—*Boll. Lab. Zool. Portici*, **4** : 347–352.

1919. Un apparechio per la preparazione della crusca avvelanata per la lotta contro le cavallette.—*Agric. colon.*, Florence, **13** : 547–553, 3 figs.

1920. Considerazoni sui rapporti biologici fra le cavalette e i loro parasiti oofagi.—*Riv. Biol.* **2** : 387–397.

PARFENTIEV, I. 1928. Report on the work of the first avio-chemical expedition of the Peoples Commissariat of Agriculture and the Aviachim. (In Russian.)—*La Défense des Plantes*, **3** (1927) : 518–532.

PARKER, J. R. 1924. Observations on the clear-winged grasshopper (*Camnula pellucida*, Scud.).—*Bull. Minnesota Agric. Expt. Sta.* **214** : 44 pp.

1925. Grasshopper migrations and modifications (Review of UVAROV, 1923).—*Ecology*, **6** : 458–459.

PARKS, T. H. 1917. A device for sowing grasshopper poison.—*J. Econ. Ent.* **10** : 524–525, 1 pl.

PAWLOWA, M. 1895. On the structure of the circulatory and sympathetic nervous system of insects, especially of Orthoptera. (In Russian.)—*Raboty Lab. zool. Varshavsk. Univ.* **1895** : 96 pp. 6 pls.

PAWLOWSKIĬ, E. N. 1914. The anatomy of *Phymateus hildebrandti*, Bol., with reference to some peculiarities of its dermal secretion. (In Russian.)—*In* DOGIEL & SOKOLOW, *Sci. Results Zool. Exped. Br. E. Africa & Uganda*, **1** : no. 3.

PETROV, S. 1905. Materials for the natural history of Acrididæ. (In Russian.)—*Izv. Moskov. Selskokhoz. Inst.* **1905** : 114–218, 13 pls.

PETRUNKEWITCH, A. & VON GUAITA, G. 1901. Über den geschlechtlichen Dimorphismus bei den Tonapparaten der Orthopteren.—*Zool. Jahrb.* Syst. **14**: 291–310, 3 pls.

PICARD, F. 1914. Les champignons parasites des insectes et leur utilisation agricole.—*Ann. Éc. Agric. Montpellier*, N.S. **13**: 121–248.

PIERANTONI, U. 1902. Contribuzione allo studio del systema nervoso stomatogastico degli Ortotteri Saltatori.—*Atti Acad. Sci. Napoli*, (2) **10**, no. 10: 8 pp. 1 pl.

1902a. Nuovo contributo alla conoscenza del systema nervoso stomatogastrico degli Ortotteri.—*Boll. Soc. Nat. Napoli*, **15**: 54–60, 1 pl.

PLOTNIKOV, V. I. 1911. Observations on the hatching of eggs of the Moroccan locust under artificial conditions and probable conclusions. (In Russian.)—*Turkestan. Selsk. Khoz.*, Tashkent, **1912**, no. 1: reprint, 12 pp.

1915. Reports on the work of the Turkestan Entomological Station for 1912, 1913, 1914 and part of 1915. (In Russian.)—Tashkent, 60 pp.

1924. Some observations on the variability of *Locusta migratoria*, L. in breeding experiments.—*Bull. Ent. Res.* **14**: 241–243.

1926. Insects injurious to cultivated plants in Central Asia. (In Russian.)—Tashkent, 292 pp. 225 figs.

1927. *Locusta* (*Pachytylus*) *migratoria*, L. and *danica*, L., as independent forms and their derivatives. (In Russian.)—Tashkent, 33 pp. 12 figs.

PORTCHINSKIĬ, I. A. 1894. On the grasshoppers damaging crops and grasses in the Perm, Tobolsk and Orenburg provinces. (In Russian.)—Dept. Agric. St. Petersburg, 131 pp. 65 figs.

1895. On the grasshoppers damaging crops and grasses in the Perm, Tobolsk and Orenburg provinces. Parasites of grasshoppers (the end). The Steppe or Russian grasshopper. (In Russian.)—Dept. Agric. St. Petersburg, 32 pp.

1914. Parasites of locusts, *Calliptamus* and injurious species of grasshoppers, from the insect world, hitherto discovered in Russia. Parasites of the order Coleoptera. (In Russian.)—*Trud. Byuro Ent. St. Petersburg*, **11**, no. 1: 68 pp. 22 figs. 2 pls.

1916. *Wohlfahrtia magnifica*, Schin. and its Russian relatives. (In Russian.)—*T.c.* no. 9: 108 pp. 39 figs. 2 pls.

POSPELOV, V. P. 1926. The influence of temperature on the maturation and general health of *Locusta migratoria*, L.—*Bull. Ent. Res.* **16**: 363–367, 2 pls.

1926a. Physiological theory of locust migrations. (In Russian.)—*La Défense des Plantes*, Leningrad, **2**: 423–435.

POULTON, E. B. 1896. On the courtship of certain European Acrididæ.—*Trans. Ent. Soc. London*, **1896**: 233–252.

PRATT, H. C. 1915. The Malayan locust (*Pachytylus* sp.).—*Bull. Dept. Agric. Fed. Malay States*, no. **24**: 42 pp. 4 figs. 16 pls. 1 map.

PREDTECHENSKIĬ, S. A. 1925. To the study of the Asiatic locust in Central Russia. (In Russian.)—*La Défense des Plantes*, Leningrad, **2**: 151–153.

PUKHOV, B. A. 1917. Poisoned baits in the control of the northern grasshoppers in the Orenburg province. (In Russian.)—*Zemled. Gaz.* **1917**, no. 15–16.

1925. Injurious Acrididæ and their control. (In Russian.)—Leningrad, 69 pp. 15 figs.

PUKHOVA, N. N. 1923. Materials to the biology of Siberian blister beetles with descriptions of their triungulins. (In Russian.)—*Izv. Sibirsk. Ent. Byuro*, no. **2**: 45–53, 1 fig.

RABAUD, E. 1915. Sur quelques réflexes des Orthoptères acridiens.—*C.R. Soc. Biol. Paris*, **78**: 668–671.

1916. Le dégorgement réflexe des Acridiens.—*Bull. Soc. zool. Fr.* **40**: 223–238.

1919. L'immobilisation réflexe et l'activité normale des Arthropodes.—*Bull. biol. Fr. Belg.* **53**: 1–49.

1923. La variation chromatique et l'homochromie des Arthropodes terrestres.—*Op. c.* **57**: 1–69.

RAEVSKIĬ, V. G. 1913. Observations on *Calliptamus italicus* in the Slavgorod district in 1922. (In Russian.)—*Izv. Sibirsk. Ent. Byuro*, no. **2**: 53–58.

RAMACHANDRA RAO, Y. 1921. *Oxya velox.*—*Rep. Proc. 4th Ent. Meeting*, Pusa, **1921**: 41–42.

RAMME, W. 1927. Die Eiablage von *Chrysochraon dispar*, Germ.—*Z. Morph. Oekol. Tiere*, **7**: 127–133, 8 figs.

Regen, J. 1911. Untersuchungen über die Atmung von Insekten unter Anwendung der graphischen Methode.—*Pflüger's Arch.* Bonn, reprint, 30 pp. 20 figs.

Regnier, P. R. 1926. Les Acridiens ravageurs du Maroc.—Dir. gén. Agric. Maroc, Rabat, 24 pp. 3 pls. figs.

R[egnier], P. R. 1926a. La lutte contre les Acridiens ravageurs.—Dir. gén. Agric. Maroc, Rabat, 24 pp. 7 pls.

Reichardt, A. N. 1923. Works of the expedition of the Narkomzem for study of parasites of Acrididæ in Siberia in 1922. (In Russian.)—*Izv. Sibirsk. Ent. Byuro*, no. **2** : 38–45.

Ribaga, 1902. Un nuovo insetto endofago *Acemyia subrotundata*, Rond., delle cavalette. *Boll. Entom. agraria*, Padua, 1902, no. 8 (abstract by Speiser, *Z. wiss. Insektenbiol.* **1**, 1905 : 480).

Ricker, D. A. 1919. Experiments with poison baits against grasshoppers.—*J. Econ. Ent.* **12** : 200–203.

Riley, C. V. 1880. *See* U.S. Entomological Commission, 2nd Report.

Ripley, L. B. 1924. Sodium fluoride as an insecticide ; its possibilities as a locust poison.—*Bull. Ent. Res.* **15** : 29–34.

Robertson, W. R. B. 1916. Chromosome studies. I. Taxonomic relationship shown in the chromosomes of Tettigidæ and Acrididæ.—*J. Morph.* **27** : 179–279, 26 pls. 4 figs.

Rockwood, L. P. 1925. On night flying and attraction to light in Acrididæ and the relation of meteorological conditions thereto.—*Pan-Pacific Ent.* **2** : 36–38.

Rodzianko, W. N. 1905. Ueber den Parasitismus der Larven von *Hypostena setiventris*, Macq., im Innern der Larven von *Tettix bipunctatus*, Linn.—*C.R. 6 Kongr. Intern. Zool. Bern*, 1905 : 696–697.

Roepke, W. 1915. Sprinkhaanenplagen.—*Teysmannia, Batavia*, **26** : 115–124, 337–358, 758–790, 7 pls. 2 figs.

1916. *Scelio javanica*, n. sp., Rpke.—*Tijdschr. Ent.* **59** : 163–169, 5 figs.

1917. Eenige opmerkingen over twee Javaansche Canthariden : *Mylabris pustulata*, Thunb., en *Epicauta ruficeps*, Ill.—*Op. c.* **60** : 252–267, 2 pls.

Rohdendorf, B. 1928. Sarcophagiden-Studien. 1. Beiträge zur Kenntnis der Gattung *Blaesoxypha*, Lw.—*Zool. Anz.* **77** : 23–28.

Röhler, E. 1906. Beiträge zur Kenntniss der Sinnesorgane der Insekten.—*Zool. Jahrb.* Anat. **22** : 225–288, 2 pls.

Rossikov, K. N. 1894. Natural enemies of the locust (*Pachytylus migratorius*, L.) in the delta of the river Terek. (In Russian.)—*Kavkaz. Selsk. Khoz.* **1894**, no. 24 : 417–418.

1895. Migratory and Italian locust in the Astrakhan province in 1895, methods of their control and natural enemies. (In Russian.)—*Astrakhan. Gub. Vedomosti*, 1895, nos. **59** & **61** : reprint, 24 pp.

1899. Migratory or Asiatic locust. Causes of disappearance of locusts from their breeding grounds and a new method of their control. (In Russian.)—Dept. Agric. St. Petersburg, 37 pp.

Rudow, F. 1870. Einige Beobachtungen über die Lebensweise der Heuschrecken. —*Z. gesamt. Naturwiss.* **1870** : 347.

Sacharov, N. L. 1913. Report on the activities of the Entomological Station in 1912. —Astrakhan, 25 pp.

Sacharov, N. L. & Schembel, S. 1914. Report on the activities of the Entomological Station in 1913.—Astrakhan, 51 pp. 17 figs.

Sajo, K. 1904. Die marokkanische Heuschrecke.—*Prometheus*, **15** : 705–709, 725–730, 740–742.

Salfi, M. 1924. Osservazioni sulla ecologia di alcuni specie di Locustidæ e Phasgonuridæ.—*Boll. Soc. Nat. Napoli*, **36** : Atti ; 129–152.

Sander, L. 1902. Die Wanderheuschrecken und ihre Bekämpfung in unseren afrikanischen Kolonien.—Berlin, 544 pp. 40 figs. 6 maps.

Schiner, J. R. 1863. Meine Ansicht über die Gattung *Blaesoxypha*, Löw.—*Verh. zool.-bot. Ges. Wien*, **13** : 1037.

Schouteden, H. 1914. Les Orthoptères nuisibles aux plantations en Afrique.—*Rev. zool. afr.* **3** : 464–470, 2 pls. 2 figs.

Schwabe, J. 1906. Beiträge zur Morphologie und Histologie der tympanalen Sinnes apparate der Orthopteren.—*Zoologica*, **20**: Heft 50, 154 pp. 5 pls.

Scudder, S. H. 1868. The songs of the grasshopper.—*Amer. Nat.* **2**: 116–120, 5 figs.

1899. The Orthopteron genus *Schistocerca*.—*Proc. Amer. Acad. Arts Sci.* **34**: 441–476.

de Seabra, A. F. 1901. As invasoes de gafanhotos em Portugal.—*Archivo Rural*, Lisbon, 1901, reprint, 25 pp. 1 pl.

Sevastianov, I. 1915. The problem of the measures for the control of the moroccan locust in Turkestan (Communications second and third). (In Russian.)—Tashkent, Turkestan Ent. Station, 88 pp.

Severin, H. C. & Gilbertson, G. I. 1917. Grasshoppers and their control.—*Bull. S. Dakota Agric. Expt. Sta.* no. **172**: 552–589, 15 figs.

Shapinskiĭ, D. V. 1923. Biological observations on the Acrididæ of the Tcheliabinsk district, Orenburg province. (In Russian.)—*Bull. Soc. Ent. Moscou*, **2**, no. 2: xxvi–xxix.

1923a. Orthopterological notes. I. The biology of *Chrysochraon dispar*, Germ. II. New parasites of Acrididæ. (In Russian.)—*T.c.* 57–69.

1924. A note on beetles of the genus *Mylabris*. (In Russian.)—*Izv. Sibirsk. Ent. Byuro*, no. **3**: 61–65.

Shimkevitch, V. 1884. The problem of transformation of Dipterous parasites in the cocoons of locusts. (In Russian.)—*Horae Soc. Ent. Ross.* **18**: 11–16.

Shull, A. F. 1911. Thysanoptera and Orthoptera of the Saginaw Bay region, Michigan.—*Michigan Biol. & Geol. Survey, Publ.* 4, Biol. Ser. **2**.

Siazov, M. M. 1912. The struggle against locusts in Turkestan. (In Russian.)—Tashkent, 197+33+16 pp. 10 pls. 1 map.

1913. The biology of the Moroccan locust. I. On the number of stages and their differences in the larvæ of the Moroccan locust. II. On the mass movements of larvæ of the Moroccan locust. (In Russian.)—*Turkestan. Selsk. Khoz.* **8**: 115–126, 2 pls. 9 figs.

von Siebold, C. T. E. 1855. Zusatz.—*Z. wiss. Zool.* **7**: 141–144.

Sjöstedt, Y. 1921. Acridiodea Australica.—*Kungl. Sven. Vetenkapsakad. Handl.* **62**: no. 3, 318 pp. 18 pls. 18 figs.

Skaife, S. H. 1925. The locust fungus, *Empusa grylli*, and its effects on its host.—*S. Afr. J. Sci.* **22**: 298–308, 1 pl.

Smith, H. E. 1915. The grasshopper outbreak in New Mexico during the summer of 1913.—*Bull. U. S. Dept. Agric.* **293**: 12 pp. 2 figs.

Sokolow, A. J. 1926. Zur Frage der Spermatophorenbefruchtung bei de Wanderheuschrecke (*Locusta migratoria*, L.). Das Weibchen.—*Z. wiss. Zool.* **127**: 608–618, 4 figs.

1926a. The structure of the female external genital apparatus of the Asiatic locust. The fate of the spermatophore. (In Russian.)—*Utchen. Zapiski Kazan. Gosud. Univ.* **86**, pt. 1, 2 (Nat. Sci.): 57–64, 11 figs.

Soldau, P. 1922. Experiments with the use of asphyxiating gases for the extermination of Acrididæ (in the summer of 1921 in Kuban). (In Russian.)—*Trud. 2 Vseross. Ent.-Phyt. S'ezda*: 9–25.

Somes, M. P. 1914. The Acrididæ of Minnesota.—*15th Rep. State Ent. Minnesota*, 98 pp. 4 pls.

Sonan, J. & Fukuda, K. 1926. Notes on the life histories of some Formosan Acrididæ. (In Japanese.)—*Trans. Nat. Hist. Soc. Formosa*, **16**, no. 82: 5–22 (abstract in *Rev. App. Ent.* A, **14**: 235–236).

South African Central Locust Bureau. 1907. First Report of the Committee of Control. Pretoria, 112 pp.

1909. Second Report, *etc.* Capetown, 86 pp.

1909a. Third Report, *etc.* Capetown, 68 pp.

1910. Fourth Report, *etc.* Capetown, 59 pp. 2 pls. 15 maps.

South Africa, Department of Agriculture. 1921. Locust destruction. 10 pp.

[Spain.] Minist. Agric., Ind., Com. y Obras publ. 1901. Memoria de la campaña contra la langosta en 1900–1901.—Madrid, 178 pp. 12 pls.

1923. Memoria de la campaña contra la langosta en 1922–1923.—Madrid, 317 pp.

Stefani Perez. *See* De Stefani Perez.

STEPANOV, P. 1880. Parasites of the locust. (In Russian.)—*Trud. Obshch. Est. Imp. Kharkov. Univ.* **13**: 102–114, 1 pl.

1881. On the metamorphosis in Diptera of the family Bombyliidæ. (In Russian.) —*Op. c.* **15**: reprint, 9 pp. 1 pl.

1882. A note on the parasites of *Stauronotus vastator*, Stev. (In Russian.)—*Op. c.* **16**: reprint, 3 pp.

STILES, CH. W. & HASSALL, A. 1920. Index catalogue of medical and veterinary zoology. Roundworms.—*Bull. Hyg. Lab. U. S. Pub. Hlth. Serv.* no. **114**: 886 pp.

SVIRIDENKO, P. A. 1922. Key for determination of stages of larvæ of the Moroccan locust. (In Russian.)—Tiflis, 6 pp.

1924. Biological observations on the Moroccan locust. (In Russian.)—Petrograd, 63 pp. 1 pl.

1926. On the work of the North-Caucasian Aviation Expedition for locust control. (In Russian.)—*Izv. Severo-Kavkaz. Kraev. Sta. Zashch. Rast.* no. **1**: 81–99.

SWENK, M. H. 1927. Further experiments with poisoned baits for grasshoppers.— *Res. Bull. Nebraska Agric. Expt. Sta.* **41**: 44 pp.

SWENK, M. H. & WEHR, E. E. 1923. Experiments with poisoned baits for grasshoppers. —*Bull. Nebraska Agric. Expt. Sta.* **183**: 28 pp.

TAKAHASHI, R. 1921. Orthoptera and water.—*Trans. Sapporo Nat. Hist. Soc.* **8**: reprint, 16 pp.

1925. Postembryonic development of *Pachytylus migratorioides*. (In Japanese.)— *Zool. Mag.*, Tokyo, **1925**: 191–203.

TIETZ, H. M. 1923. The anatomy of the digestive system of the Carolina locust (*Dissosteira carolina*, Linn.).—*Ann. Ent. Soc. Amer.* **16**: 256–268, 5 pls.

TOWNSEND, C. H. T. 1928. *Schistocercophaga*, new genus of locust parasites.—*Ent News*, **39**: 152.

TRABUT, L. 1891. Les champignons parasites du criquet pélerin.—*Rev. gén. bot.* Paris, **3**: 401–405, figs.

TRÄGÅRDH, I. 1905. Acariden aus Ægypten und den Sudan.—*Res. Swed. Zoolog. Exped. Egypt & White Nile*, Upsala, **2**: 67–68.

1908. Acarini in: SJÖSTEDT. Kilimandjaro-Meru Expedition, **20**, 3: 31–57, 2 pls.

TREHERNE, R. C. & BUCKELL, E. R. 1924. Grasshoppers of British Columbia.—*Bull. Dept. Agric. Canada*, no. **39** (Ent. Bull. 26): 40 pp. 18 figs. 3 pls.

TROITSKIĬ, D. 1914. Acridid pests in the Semipalatinsk province in 1912. (In Russian.) —*Nuzhdui Zapad.-Sibirsk. Selsk. Khoz.* **2**, no. 1: 23–49.

United States Entomological Commission. 1878. First annual report. 477+294 pp. 105 figs. 5 pls. 1 map.

1880. Second report. 322 pp. 19 figs. 16 pls. 6 maps.

1883. Third report. pp. 1–85, 2 maps.

UVAROV, B. P. 1911. Migratory locust in the Stavropol province in 1911. (In Russian.) —*Zashch. Rast. ot vred.* (Suppmt. *Lyubit. Prirodui*), no. **3** (7): 13–22, figs.

1915. Essays on locust control. (In Russian.)—*Selsk. Khoz. i Lesov.* **247**: 266–281, 377–411; **248**: 31–47.

1921. A revision of the genus *Locusta*, L. (*Pachytylus*, Fieb.), with a new theory as to the periodicity and migrations of locusts.—*Bull. Ent. Res.* **12**: 135–163, 8 figs.

1922. Rice grasshoppers of the genus *Hieroglyphus* and their nearest allies.—*Op. c.* **13**: 225–241, 3 figs.

1923. Note on locusts of economic importance, with some new data on the periodicity of locust invasions.—*Op. c.* **14**: 31–39, 1 fig.

1923a. Quelques problèmes de la biologie des sauterelles.—*Ann. Epiph.*, Paris, **9**: 84–108.

1926. Notes on the genus *Oxya*, Serv.—*Bull. Ent. Res.* **17**: 45–48.

VALOVA, A. V. 1924. Feeding habits of *Stenobothrus morio*, Fabr., and of other northern grasshoppers. (In Russian.)—*Izv. Sibirsk. Sta. Zasch. Rast.*, Novonikolaevsk, no. **1** (4): 16–35.

VAN DER MERWE, C. P. & KENT, C. C. 1925. The elegant grasshopper (*Zonocerus elegans*, Thunb.).—*J. Dept. Agric. S. Afr.* **10**: 29–42.

VAYSSIÈRE, P. 1919. Observations biologiques sur *Dociostaurus maroccanus* en Crau.— *Bull. Soc. zool. Fr.* **44**: 359–363.

1921. La lutte contre le criquet marocain (*Dociostaurus maroccanus*, Thunb.) en Crau en 1920).—*Ann. Epiph.*, Paris, **7**: 117–177, 11 pls.

VAYSSIÈRE, P. 1921a. La lutte contre les sauterelles.—*Les Intéréts Marocains*, Paris, **3**, no. 43 : 3–4 ; no. 44 : 13–15.

1924. Le probleme acridien et sa solution internationale.—*Matér. Etude Calamités*, Geneva, no. **2** : 122–161.

VAYSSIÈRE, P. & MIMEUR, J. 1925. Les Orthoptères nuisibles au Cotonnier et autres cultures en Afrique occidentale française.—*Agron. colon.* no. **89** : 202–224, 3 pls.

VESTAL, A. G. 1913. Local distribution of grasshoppers in relation to plant associations.—*Biol. Bull. Woods Hole, Mass.* **25** : 141–180.

VIALLANES, H. 1887. Etudes hystologiques et organologiques sur les centres nerveux et les organes des sens des animaux articulés. I. Le cerveau du criquet.—*Ann. Sci. nat., Zool.* (7) **4** : 1–98, 5 pls.

VILLOTT, A. 1891. L'évolution des Gordiens.—*Ann. Sci. nat., Zool.* (7) **11** : 327–401, 3 pls.

VINAL, S. C. 1919. The respiratory system of the Carolina locust.—*J. N. York Ent. Soc.* **27** : 19–32, pls.

VINOKUROV, G. M. 1916. From biological observations on the migratory locust. (In Russian.)—*Rep. Stavropol Ent. Byuro*, **1914** : Petrograd, 84–101, figs.

1927. Grasshoppers and areas of their outbreaks in Eastern Siberia. (In Russian.) —*Bull. Irukutsk Plant Prot. Sta.* **1** : 3–52.

VORONTZOVSKIĬ, D. 1924. To the study of Acrididæ. (In Russian.)—*Sovetsk. Kirgiziya*, Orenburg, no. **11–12** : 137–144.

1926. New cases of parasitism in Acrididæ. (In Russian.)—*La Défense des Plantes*, Leningrad, **3** : 280.

1926a. Materials to the study of egg-pods of Acrididæ.—*Trud. Obshch. Izutchen. Kazakst.*, Kuizuil Orda, **7**, pt. 1 : reprint, 8 pp. 3 figs.

VOSSELER, J. 1902. Beiträge zur Faunistik und Biologie der Orthopteren Algeriens und Tunisiens.—*Zool. Jahrb.* Syst. **17** : 1–79, 3 pls.

1905. Die Wanderheuschrecken in Usambara im Jahre 1903/1904, zugleich ein Beitrag zu ihrer Biologie.—*Ber. Ld.- u. Forstw. D.-Ostafr.* **2** : 291–374, 2 pls.

VYSHELESSKY, N. S. 1927. On the reactions of locusts towards dusted plants. (In Russian.)—*La Défense des Plantes*, Leningrad, **3** : 533.

WALKER, E. M. 1919, 1922. The terminal abdominal structures of Orthopteroid insects. A phylogenetic study.—*Ann. Ent. Soc. Amer.* **12** : 267–316, 9 pls. ; **15** : 1–76, 11 pls.

WASHBURN, F. L. 1912. Grasshoppers and other injurious insects of 1911 and 1912.— *14th Rep. State Ent. Minnesota :* 1–43.

WATSON, M. E. 1916. Studies on Gregarines.—*Illinois Biol. Monog.* **2**, no. 3 : 258 pp. 15 pls.

WEBB WARE, F. C. 1915. Locusts in Baluchistan.—*Agric. J. India*, **10** : 159–166. 2 pls. map.

WERHLE, L. P. & WELCH, P. S. 1925. The occurrence of mites in the tracheal system of certain Orthoptera.—*Ann. Ent. Soc. Amer.* **18** : 35–44.

WERNER, F. 1894. Zoologische Miscellen. Die relative Darmlange bei Insekten- und pflanzenfressenden Orthopteren.—*Biol. Centralbl.* **14** : 116–119.

WEYENBERGH, G. H. 1876. La langosta y sus enemigos.—*Informe An. Dep. nac. Agric. Argentina*, **1875** : 451–480, 2 pls.

WILLEMSE, C. 1925. Revision der Gattung *Oxya*, Serville.—*Tijdschr. Ent.* **68** : 1–60, 65 figs.

WILLIAMS, R. H. 1926. Fighting the locust.—*Fmg. S. Africa*, **1** : 339–340.

WILLIS, J. A. 1925. Effects of different tensions of carbon dioxide on certain Orthoptera. —*Biol. Bull. Woods Hole, Mass.* **48** : 209–223, 5 figs. 5 tables.

YERSIN, A. 1854. Mémoire sur quelques faits relatifs à la stridulation des Orthoptères et à leur distribution géographique en Europe.—*Bull. Soc. vaud. Sci. nat.* **4**, no. 34 : 108–129, 2 pls.

YUASA, H. 1920. The anatomy of the head and mouth parts of Orthoptera and Euplexoptera.—*J. Morph.* **33** : 251–286, 9 pls.

ZACHAROV, L. Z. 1927. Lower reaches of the river Kuma as breeding grounds of the migratory locust. (In Russian.)—*Bull. North Caucas. Plant Prot. Sta.* Rostov-Don, **3** : 3–92, 2 pls. 1 map.

ZACHER, F. 1926. Orthopteren. Geradflügler.—SORAUER, *Hand. Pflanzenkr.* 2 Aufl. **4** : 150–237, figs.

INDEX

The attention of readers of the special part of this book should be drawn to the fact that supplementary information on the species discussed in detail in the respective chapters is scattered throughout the general part. In the following index the pages on which a species is treated fully are indicated in Clarendon type, and references to all pages containing additional data on it are given in ordinary type. The index includes also a number of species of ACRIDIDÆ not described fully in the special part, but mentioned in the general chapters, as well as their natural enemies. It has been found, however, superfluous to include in the index all the names of the latter, since species belonging to certain groups (*e.g. Mylabris*, SARCOPHAGINÆ, etc.) will be found together in the text, and one general reference is sufficient. Synonyms under which some species of locusts and grasshoppers are mentioned in the literature are also included in the index, with cross-references to their correct names.

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PLATE I

1. Skins shed by larvæ of *Calliptamus italicus* at hatching. (Photo by A. N. Kiritchenko.)
2. Hoppers of the last stage of the Moroccan locust on wheat. (Photo by the Stavropol Entomological Bureau.)

PLATE I

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2

PLATE II

Four stages of the final moult of *Locusta migratoria*. (Photo by the Stavropol Entomological Bureau.)

PLATE II

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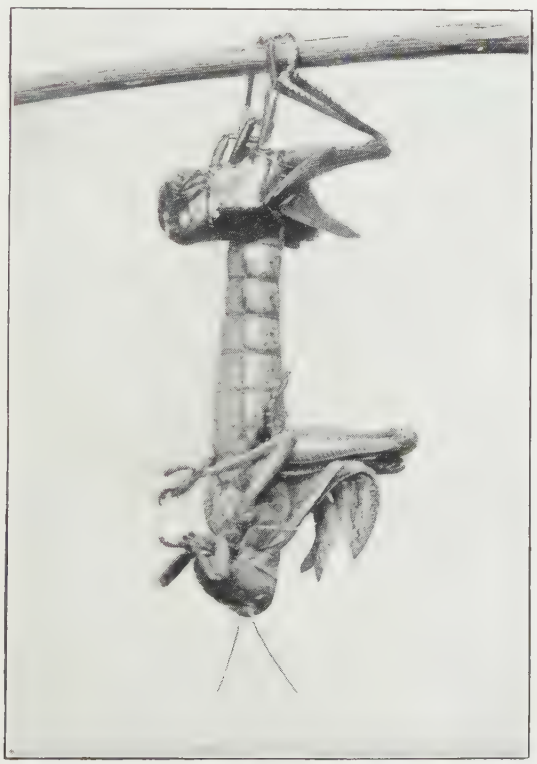

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PLATE III

Internal organs of *Locusta migratoria*, ♂, on the first day of the imaginal stage (after Pospelov).

1. Air-sacs.
2. Fat-body.
3. Testis.
4. Accessory glands.

PLATE III

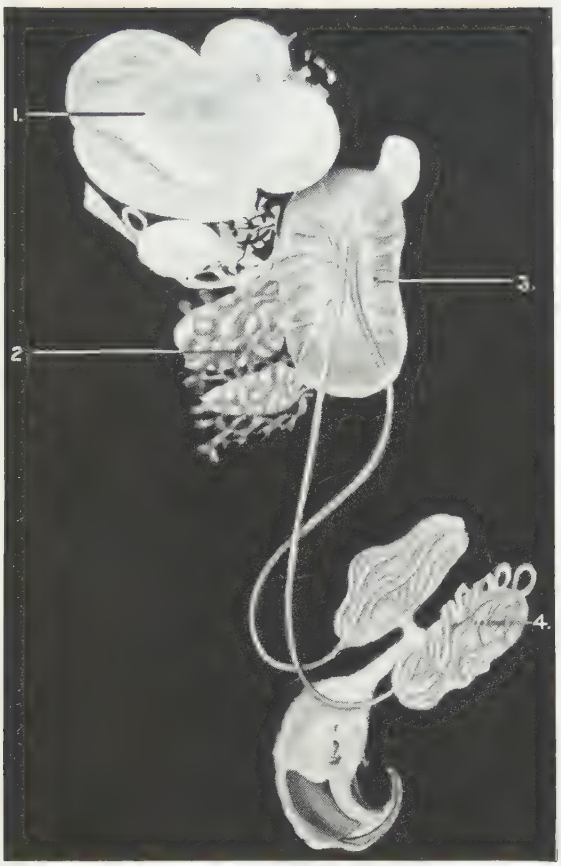

PLATE IV

1. Ovaries of *Locusta migratoria* on the first day of the imaginal stage. ×10.
2. Collapsed air-sacs of *L. migratoria* after migration. ×10.
3. Fat-body of the imago of *L. migratoria* during diapause. (All after Pospelov.)

PLATE IV

1

2

3

PLATE V

A flying swarm of the Brown Locust (after Somes).

PLATE V

PLATE VI

1. Typical breeding place of the Moroccan Locust in Anatolia.
2. Primary bands of hoppers of the Moroccan Locust.
3. A group of hoppers of the Moroccan Locust warming themselves in the sun on a stone. (All after La Baume.)

PLATE VI

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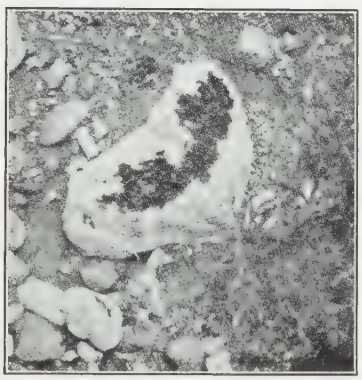

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PLATE IX

Hoppers of the Desert Locust.

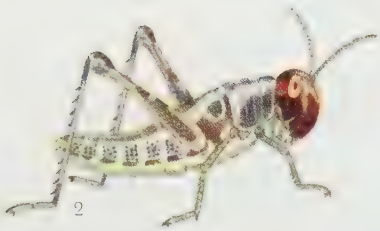
1–5. Swarming phase. 1*a*–5*a*. Solitary phase.

(Redrawn from a plate to be published by the Wellcome Tropical Research Laboratories, Khartoum.)

PLATE IX

1

1a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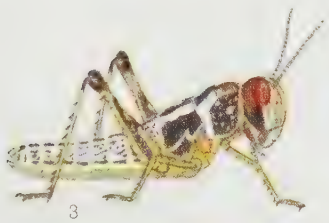
2a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3a

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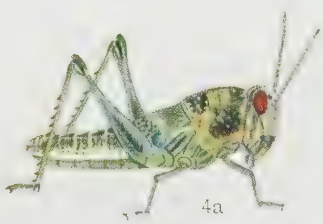
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5a

566 120164 7 104